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EFFECTS OF DIFFERENT INTENSITIES OF CLIPPING ON SHORT GRASSES IN WEST-CENTRAL KANSAS

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INTRODUCTION

Since appearance of the buffalo (*Bison bison bison* (L)), vegetation of the Great Plains has been subjected to various degrees of utilization. It is probably safe to assume that at least moderate use was common, and that grazing was most intense during dry cycles or when population of the buffalo was greatest. As the pioneer white man occupied the plains region, the number of livestock gradually increased. Also, during this period vast amounts of prairie sod were plowed up for growing wheat and other crops, thereby reducing the area left in native vegetation.

Little attention was given to intensity of grazing until the great drought of the 1930's when production of native vegetation suffered an alarming reduction. During this disastrous period, the most mesophytic plants survived only in favored locations, and even the most xerophytic species were greatly reduced in both abundance and frequency under heavy use by livestock. Also, the yield of native vegetation which at one time probably averaged from 2,000 to 3,000 pounds per acre, was suddenly reduced to little more than 100 pounds (Weaver and Albertson 1944). This tragic experience caused federal and state agencies, as well as individuals, to give serious thought to the ecology and economics of overuse on grasslands.

The college pasture, an area of 830 acres of mixed prairie (Albertson 1937), was selected for study to determine effects of various intensities of clipping upon the most important grasses. The investigation was conducted on a portion of the pasture dominated by short grasses since this is the most common type of prairie vegetation of the Great Plains.

METHODS

An upland area of about one-fourth acre was fenced in the spring of 1942 to exclude livestock. The experimental plot consisted of 2 square areas, each of which contained 36 one-meter quadrats. The quadrats were arranged into 6 series with 6 quadrats in each series. Lanes between the quadrats were 2 feet wide. The 6 quadrats in each series were evenly distributed among the 36 in the square. All quadrats in each series were clipped alike but each series was clipped at different intensities. For example, in one square (treatments A to F inclusive) rate of clipping was as follows:

A. Unclipped.
B. Clipped every 6 weeks beginning June 25, at a height of 2 inches on 60 per cent of the area. Remainder of the area unclipped.
C. Clipped every 4 weeks, beginning June 10, at a height of 1.5 inches on 80 per cent of the area.
D. Clipped every 3 weeks, beginning June 5, at a height of 1 inch on 90 per cent of the area.
E. Removal of all growth every 2 weeks, beginning May 25.

F. Deferred until July 31 after which clipped every 2 weeks, first at 4 inches, then 3 inches, then 2 inches, then 1 inch and finally complete removal on September 25.

On the other area of 36 quadrats (treatments G to L inclusive) clipping was usually slightly more intense on each series than on its counterpart in treatments A to F.

All old growth was removed on May 15, 1942, before the experiment was begun. Previous to each harvest, measurements were made to determine increment of top growth since the previous clipping. Notes were also taken on general growth conditions. Yields in pounds per acre were obtained by hand-clipping the vegetation. Amount of grasses not removed by clipping was determined by use of a utilization gauge or by clipping similar areas outside the experimental plot. Samples of grasses were retained for chemical analysis to determine effect of clipping on protein content. Basal cover was charted with a pantograph each spring and fall and later planimetered to determine per cent cover.

Soil moisture to a depth of 5 feet was determined each week from soil samples taken with a geotome. Per cent moisture above hygroscopic coefficient was considered amount available for plant growth. Relative humidity and air temperature records were obtained from a hygro-thermograph. Precipitation and evaporation from a free water surface were taken from records of the United States Weather Bureau.[1]

In the fall of 1942, 1945, and 1947, trenches to the depth of root penetration were dug around columns of sod on areas which were unclipped (A), moderately clipped (D), and closely clipped (E). The columns of sod were cut into blocks 4 inches in length and the roots were washed out of the soil, counted, air dried, and weighed.

Clipping was discontinued in the fall of 1946 on one square area (G–L) and in 1947 on the other square. Observations and measurements were made every year until 1950 to determine rate of recovery.

[1] Climatological Data, U. S. Department of Commerce, Weather Bureau, Topeka, Kansas.

Related Studies

During the past 2 decades much work has been done to determine effect of clipping upon plant production and survival.

Black *et al.* (1937) found that blue grama (*Bouteloua gracilis* (H.B.K.) Lag. ex Steud.) and buffalo grass (*Buchloë dactyloides* (Nutt.) Engelm.) were both affected much less by clipping than were western wheatgrass (*Agropyron smithii* Rydb.) and plains bluegrass (*Poa arida* Vasey). Both species produced much less forage when clipped at 10-day intervals then when clipped at 30 or 40 day intervals. Western wheatgrass produced the most forage when clipped only at the end of the grazing season. Total production on all the forage plants was greatest on plots clipped at 40-day intervals and was more than double that on those clipped at 10-day intervals.

Aldous (1930), in eastern Kansas, found that removal of vegetation at short intervals caused a much greater decrease in density than did removal at longer intervals.

Riegel (1947), in western Kansas, found the taller native grasses to be more susceptible to clipping than were the shorter ones. In every case where the grasses were clipped for several months, there was an increase in total height but a decrease in weight.

In New Mexico, Nelson (1934) found that, when heavily grazed year after year, the stand of black grama (*Bouteloua eriopoda* (Torr.) Torr.) rapidly broke down and eventually died. Natural revegetation was also seriously handicapped because of the low density and poor vigor of the old plants and excessive trampling of new plants. Drought losses were also intensified.

Biswell and Weaver (1933) studied the effects of removal of tops of certain grasses on root growth and yield of top growth.

The yield when clipped at two-week intervals in comparison to yield when clipped at end of season ranged from 14.5 per cent in big bluestem (*Andropogon gerardi* Vitman) to 63.1 per cent in buffalo grass. The species with greatest reduction in yield of tops also had the least root growth.

Studies by Weaver and Hougen (1939) disclosed that little bluestem (*Andropogon scoparius* (Michx.) in quadrats closely cut the preceding year was only one-half as tall as that in the controls where it averaged 2.5 inches.

Tomanek (1948) studied 5 pastures in western Kansas where grazing intensity had been different during the previous 15 years. He found yield on the moderately grazed pasture to be significantly greater than on the ungrazed or heavily grazed pastures.

Weaver (1930), in eastern Nebraska, reported that over-grazing resulted in poor root growth and permitted little food accumulation. Plants with poorly established root systems and little stored food were not resistant to winter-killing. In another paper (Weaver 1950), it was shown that the quantity of roots in an over-grazed pasture was only 42 per cent as much as on a high grade area.

Stoddart (1946) found that when *Agropyron spicatum* (Pursh) Scribn. and Smith was clipped during the period of active reproduction it suffered higher percentage of death and yielded less forage than when clipped early or not until the end of the growing season.

In Utah, McCarty and Price (1942) found that the quantity of carbohydrate reserves in the plants at the end of the growing season appeared to be influenced more by time and degree of clipping than by frequency. Early growth in the spring was dependent upon reserve foods in the plants.

The results of McCarty and Price agree in general with those of Graber (1931) in Wisconsin where he ran clipping studies on Kentucky blue grass (*Poa pratensis* L.) and other grasses. Here it was found that the quantity of subterranean growth and total weight of tops varied inversely with frequency of defoliation.

Sturkie (1930), in Alabama, reported that Johnson grass (*Sorghum halepense* (L.) Pers.) usually developed rootstocks after the heads appeared. Any cutting treatment reduced the rootstock development, and the more frequently the cutting was made the greater was the reduction.

Environment

The great drought closed in 1939. Precipitation in 1940 was normal (22.91

Table I. *Precipitation at Hays, Kansas, from 1942 to 1947 with deviation from normal*

Year	Month						Growing season	Annual
	April	May	June	July	Aug.	Sept.		
1942	4.74 +2.45	4.92 +1.46	7.04 +2.94	2.90 − .27	2.88 − .26	.94 −1.33	23.42	29.6
1943	1.45 − .84	2.52 − .94	1.01 −3.09	2.83 − .34	2.69 − .45	2.32 + .05	12.82	16.2
1944	4.71 +2.50	2.77 − .74	1.08 −3.01	6.78 +3.91	5.43 +2.35	.44 −1.83	21.21	29.7
1945	3.63 +1.42	3.78 + .27	5.29 +1.20	1.67 −1.20	1.69 −1.39	1.40 − .87	17.46	20.34
1946	1.03 −1.18	6.47 +2.96	1.05 −3.04	2.18 − .69	1.73 −1.35	4.92 +2.65	17.38	26.48
1947	2.22 + .01	5.31 +1.80	6.98 +2.89	.87 −2.00	2.06 −1.02	.08 −2.19	17.52	22.65

inches) but because of the unusually dry soil resulting from the drought, no recovery in vegetation occurred until later in this season. During 1941, however, total precipitation was approximately 6 inches above normal and the original cover was partially restored. This problem, therefore, was initiated before replacement of previous cover was complete.

Conditions for growth were excellent during the growing season of 1942. Precipitation during this year was 29.6 inches —nearly 7 inches above average. Total rainfall for the growing season was 23.4 inches which also was well above average (Table I). April, May, and June were especially wet and during this time available soil moisture was restored to a depth of 5 feet (Fig. 1). Decreased rainfall during July, August, and September, however, caused a reduction in available soil moisture but not sufficient to materially retard growth of vegetation. Average maximum relative humidity for the period of late June to early September was above 90 per cent. Average minimum for the same period was 55.5 per cent. Evaporation from a free water surface was 66.8 inches for the season.

Conditions for growth during 1943 were in sharp contrast to those of the previous year. Annual precipitation was only 16.2 inches and for the growing season 12.8 inches. Soil moisture in May was nearly the same as in the previous September, but during June, July, and August scarcely any was available for plant growth except occasionally in the top 6 inches. Evaporation from a free water surface (82.6 inches) was also unusually high during this year. Maximum relative humidity for the growing season averaged only 76.5

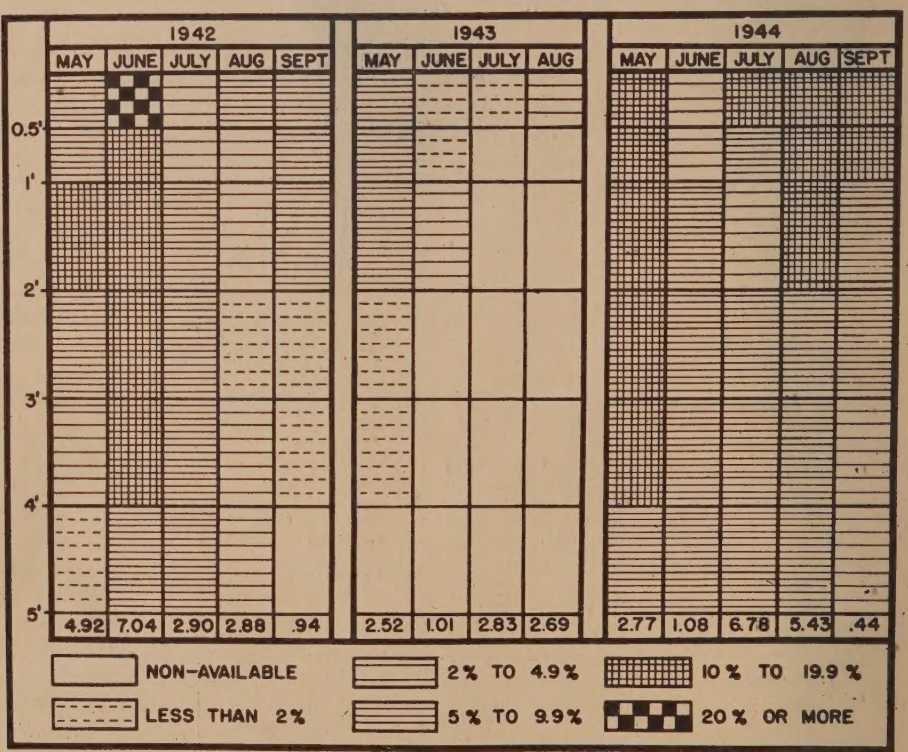

FIG. 1. Available soil moisture to a depth of five feet in blue grama-buffalo grass sod. 1942–1944, Hays, Kansas.

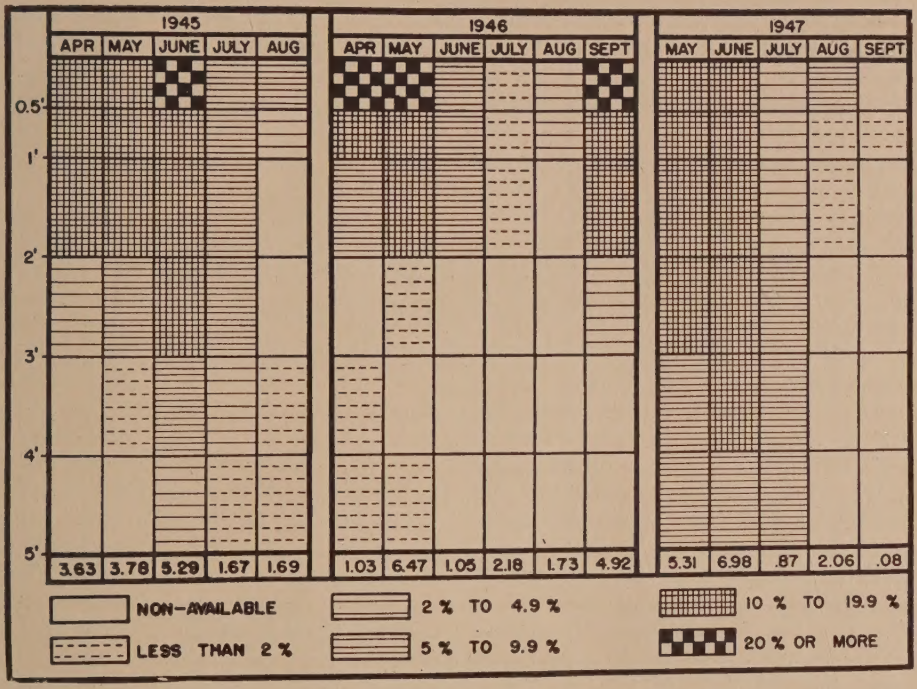

FIG. 2. Available soil moisture to a depth of five feet in blue grama-buffalo grass. 1945–1947, Hays, Kansas.

per cent and the average minimum dropped to 34 per cent.

Conditions for growth during 1944 were nearly ideal. Precipitation was relatively high; evaporation and wind velocity were relatively low, and temperatures were normal. Available soil moisture was never deficient.

The growing seasons of 1945 and 1947 were similar in that precipitation was above normal during the early part of each season and that droughts occurred during July, August, and September of both years. Available soil moisture in the top 24 inches was sufficient for plant growth through most of the season of 1945; however, in 1947, there was a deficiency of soil moisture in August and September (Fig. 2). Relative humidity data are not available for 1945, but for the growing season of 1947 the maximum averaged 86.5 per cent and the average minimum 50.6 per cent.

The season of 1946 was unfavorable to growth of vegetation due to distribution of rainfall rather than to total amount received. For example, precipitation during April was more than one inch below normal; May rainfall was nearly 3 inches above normal, but drought was severe during June, July, and August. September was wet, but this was too late to cause much renewal of growth of vegetation. Available soil moisture was seldom present below 24 inches. Above this depth there was an abundance of soil moisture during April, May, June, and September, but in July and August there was scarcely any available. Average maximum relative humidity for the season was only 81.8 and the low 38.3 per cent.

VEGETATION

Cover of vegetation was composed primarily of the two short grasses, blue grama and buffalo grass but as reported

in more detail later, the replacement of cover had not been complete following the drought which closed in 1939. Sand dropseed (*Sporobolus cryptandrus* (Torr.) A. Gray), which in former years had invaded many open spaces, was still present in small bunches. Six-weeks fescue (*Festuca octoflora* Walt.), the annual interstitial, was present only in small quantities. Little barley (*Hordeum pusillum* Nutt.) was common especially in years when soil moisture in fall or spring was sufficient to support germination of seed. These weedy grasses and several annual forbs were harvested each year early in the season in order to remove their competition with the plants under study. Yields averaged from 80 to 300 pounds per acre each season. Several species of perennial forbs that had survived the drought were scattered among the short grasses on the hill top. Most common were salmon-colored mallow (*Malvastrum coccineum* (Nutt.) A. Gray) and wild alfalfa (*Psoralea tenuiflora* Pursh). These were clipped at the time of each harvest. Yield of forbs seldom exceeded 100 pounds per acre.

Results

Data from the general notes and measurements of growth made regularly through each season are presented under each year from 1942 to 1947. Other results are given under the respective headings.

Description of top growth

1942

Growth was rapid in the spring of 1942 when soil moisture was plentiful. Measurements made during early June revealed that the unclipped blue grama plants were 7 inches tall and those of buffalo grass 5 inches. On the closely clipped areas, however, top growth to date was 10 inches and 7 inches, respectively, on blue grama and buffalo grass. In early July, unclipped foliage of the two grasses was still green but had grown less than 2 inches during the past month. Many of the closely clipped blue grama blades were light green in color and were slightly shorter than others which were dark green; buffalo grass, however, showed no signs of damage due to clipping.

In early September, heads of blue grama were formed on flower stalks 12–16 inches high. Tips of foliage were beginning to ripen on unclipped areas, whereas, no ripening was found under moderate to heavy clipping; in fact it was evident that, on buffalo grass, moderate clipping not only stimulated continuous growth of foliage but also production of both staminate and pistillate flower stalks. Under heavy clipping, blue grama tillers were green but slender and sparse. Buffalo grass had produced a small crop of seed on very short flower stalks. Last measurements of the season made in early October disclosed semi-dormancy on unclipped and lightly clipped areas. On more heavily clipped areas, however, succulence was high and 1–2 inches of growth had occurred during the previous two weeks.

The measurements in length of growth made on each clipping date were totaled at the close of each season. In order to more clearly show trends on clipping effects, total increment of top growth is given for each year on areas heavily clipped (E), moderately clipped (D), lightly clipped (C), very lightly clipped (B), and unclipped (A) (Fig. 3). It was apparent that increment of growth between clippings during the first year of study was greatly stimulated on the closely clipped areas. Total growth on E during the season was 19.8 inches. It was only about 2 inches less (17.6) on D, but on C it was only 12.3 inches. This was 5 inches greater than on A, the unclipped location and also on B, which was very lightly clipped.

1943

The season of 1943 was greatly different from that of 1942. The impact of low

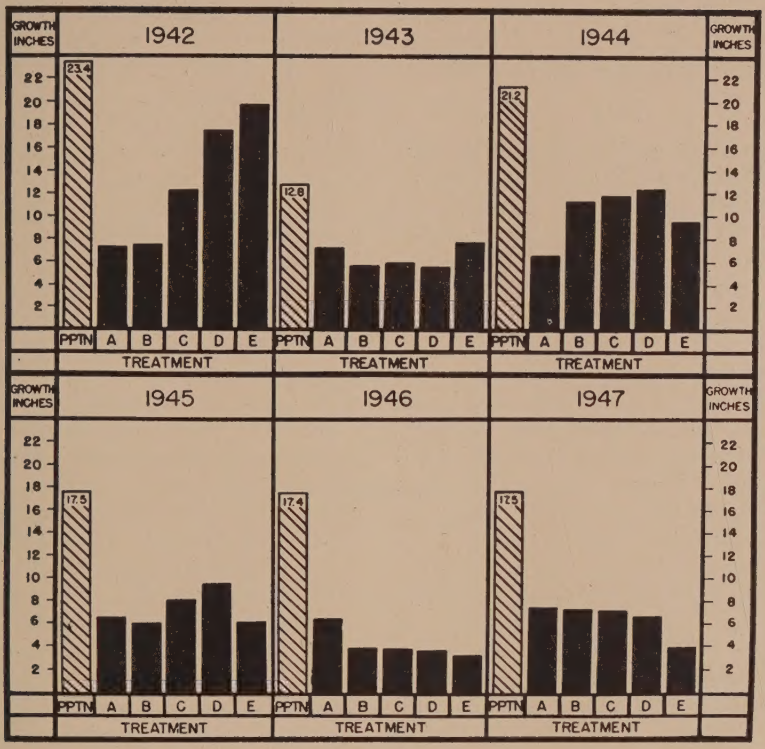

FIG. 3. Increment of top growth for treatment A to E inclusive for 1942 to 1947. Seasonal rainfall (pptn) is given for each year.

total precipitation for the year was intensified by unfavorable distribution, especially during the growing season. Observations were first made on May 6 and at that time all grasses were showing signs of drought.

Effect of drought was even more apparent on July 9 when the unclipped blades, having died back through half their length, were semi-dormant. Blades of blue grama had rolled tightly and had assumed a grayish color. Under heavy clipping, the drought stricken semi-dormant blades had grown very little since last clipped.

Rains, totaling 1.50 inches, occurred in mid-July but moisture penetrated the soil to a depth of only 4 inches. By July 22, the unclipped blades were 6–8 inches long. The youngest blue grama leaves nearest the top of the stem were green but those that arose from the nodes lower down were nearly dead.

In general appearance, the unclipped area had a yellow overcast with a green undertone. Closely clipped areas, however, were much greener than were the longer blades on unclipped grasses. Comparatively few staminate and pistillate flowers were being formed on buffalo grass. Blue grama flower stalks, however, were forming but none had emerged from the sheaths. When moderately clipped, growth seemed more vigorous than on unclipped or lightly clipped areas. Even on closely clipped areas, growth was nearly as great in 2 weeks as in 6 weeks under light clipping.

During this very dry year, increment on E was 7.7 inches which was approxi-

mately .5 inch more than on the unclipped area. On B, C, and D, total increment was 6 inches or slightly less (Fig. 3).

1944

High rainfall during the growing season of 1944 furnished nearly optimum soil moisture for growth of vegetation. Early in June, buffalo grass on unclipped areas was 6–7 inches high and blue grama about 1 inch higher. However, on heavily clipped vegetation the height was only 2–3 inches.

On unclipped areas, buffalo grass seed was fairly heavy on seed stalks 2–3 inches long; under moderate clipping a slightly heavier seed set was found on stalks 1–2 inches tall. Where clipping had been very short, the heavy seed yield was borne on stalks less than 1 inch in length.

Maximum height on unclipped areas was reached by early July and loss of succulence was evident through remainder of the season. On moderately clipped areas, however, vegetation remained green and diminished growth was maintained until late September. Under heavy clipping the weakened vegetation was green and produced a small amount of growth throughout the season.

During this season, with rainfall similar to that in 1942, increment on E was only 9.5 inches—about 10 inches less than in 1942. Growth on treatment A was nearly 7 inches, which was about its average for the period of study. On the other three areas, however, it ranged from 11.3 inches on B to 12.3 inches on D. These results indicate that close clipping on E was not furnishing as much stimulus to growth as was lighter clipping on B, C, and D.

1945

In the spring of 1945, an accidental fire swept across the experimental plot and considerable damage resulted where debris had been allowed to accumulate from growth of previous years (Hopkins *et al.* 1948). The fire killed many blue grama and buffalo grass crowns embedded in the debris. Consequently, the number of tillers per unit area was far less than normal. Live tillers grew rapidly and in late May had reached a height of 5 inches. On moderately clipped vegetation fire damage was relatively small and growth of grasses was normal.

Three years of heavy clipping had seriously weakened both blue grama and buffalo grass plants. Most of the former had been killed and what remained alive were so weakened that only a few scattered tillers were found. Where clipping was close, pistillate flowers of buffalo grass were borne on exceedingly short stalks.

By early September, effect of clipping was becoming increasingly evident. Semidomancy seemed to prevail even where clipping had been only moderately heavy. Deleterious effects of clipping were much more evident on closely clipped grasses than elsewhere. Here breakdown was alarming as indicated by dead or semidead crowns of both dominants. Blue grama had suffered considerably more than buffalo grass. Crowns with sparsely populated, feebly growing tillers were common on mounds .5 inch or more in height. Drought and heavy clipping, indeed, had taken their toll.

Rainfall during the seasons of 1945, 1946, and 1947 differed but little in amount, but, as mentioned under environment, poor distribution in 1946 affected greatly the amount of growth for the season. In 1945, close clipping during previous years had so weakened the grasses that increment for the season was less than on all other treatments except B. No significant difference in height of growth was found in treatments A, D, and E. On C and D, however, there was considerable clipping stimulus. For example, total increment for these treatments was respectively 8 and 9.4 inches in comparison to only 6 inches or slightly more on other treatments.

1946

Available surface soil moisture in the spring of 1946 supported normal growth

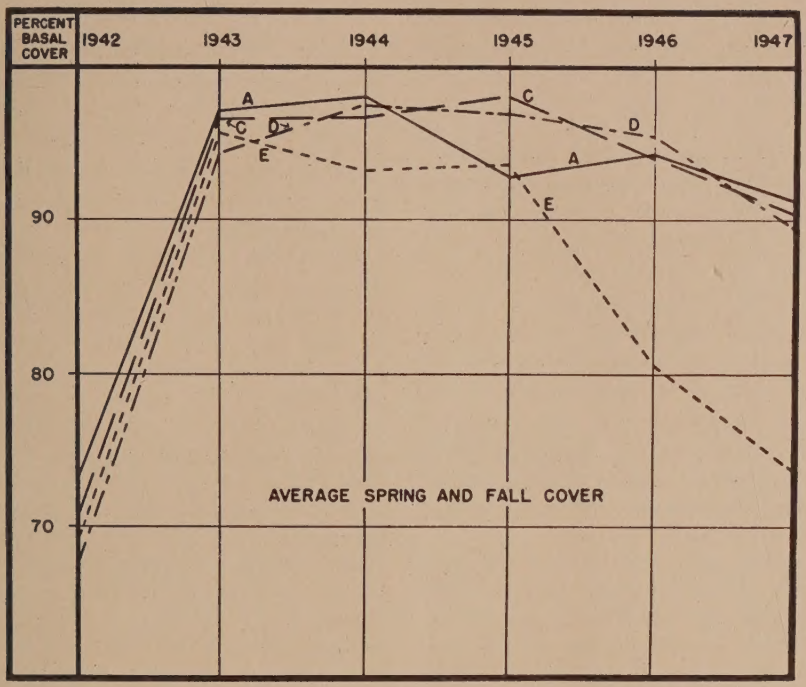

FIG. 4. Average spring and fall cover for 1942 to 1947 on treatments A, C, D, and E.

of short grasses on unclipped areas. On June 1, buffalo grass blades were 5 inches long and there were relatively few staminate flower stalks 4 inches in height. Very little buffalo grass seed was produced. With increased clipping, height of foliage and staminate flower stalks became less. For example, on June 1, leaves and staminate flower stalks on moderately clipped areas were over 3 inches long, and some buffalo grass stolons reached 10 inches in length. Where clipping was heaviest, however, length of blades was only 1 inch on buffalo grass and slightly less on blue grama. Most crowns had dead centers and a few small tillers coming from nearly dead tissue on the periphery. Buffalo grass stolons 10 inches long were entering the closely clipped areas from plants in the surrounding lanes where growth was normal. Stolons developed from plants within the clipped areas, on the contrary, were sparse and usually never exceeded 2 inches in length. Poorly developed buffalo grass seed was abundant in all heavily clipped areas. Except under the crowns, sheet erosion had removed nearly 1 inch of the surface soil.

The small amount of available soil moisture during June and July caused decreased growth of the unclipped grasses and by August they were completely dormant except near the soil surface where green tissue still persisted. Dormancy was also common under moderate clipping. Where removal was heaviest, however, the grasses remained green but no growth was occurring. It was evident that more of the crowns were dead than earlier in the season, indicating that the grasses were continuously becoming weaker due to nearly complete removal of top growth. Increased soil moisture in September (Fig. 2) stimulated a small amount of growth on all treatments. In-

crement for the season ranged between 6.5 inches on treatment A to 3.2 inches on E.

1947

Clipping on one series of quadrats was discontinued at the close of the season of 1946 in order to make studies on roots as affected by clipping. On the other series, however, notes and clippings were continued in 1947. It was evident that closely clipped areas had suffered further breakdown but not to the extent of the two previous years. A good supply of soil moisture in spring and early summer doubtless decreased the damaging effects of close clipping. Tillers were sparse and weak but they remained green throughout most of the season.

Under all treatments growth was considerably more vigorous than in 1946. Where clipping was heaviest grasses retained their succulence but growth was significantly less than under lighter clipping.

Increment in 1947 was considerably greater than in 1946, except on E where clipping was heaviest. Here growth was only 4 inches. On the other treatments, increment varied inversely with intensity of clipping. The difference, however, was relatively small. It seemed evident that close clipping had decreased growth greatly on E and only slightly on B, C, and D.

Basal Cover

In 1932, basal cover of shortgrass prairies averaged approximately 90 per cent (Albertson 1937). During the great drought of 1933 to 1939, cover was reduced to some 20 per cent in well-managed pastures and much lower than this where heavy stocking was common.

When the study was initiated in the spring of 1942, cover averaged between 40 and 50 per cent. It was well above 90 per cent, due mostly to growth of buffalo grass, when determined in the fall of the same year. This made an average of spring and fall cover of approximately 70 per cent on all treatments (Fig. 4). The high average cover in 1943 was not due to growth during that year but rather to a maintenance of what was produced in 1942. Effect of clipping upon cover did not occur until 1944 when E, the heavily clipped area, lost about 2 per cent. No further loss occurred until 1946 when the cover dropped to approximately 80 per cent. In 1947 cover was further reduced to 74 per cent.

On C, the cover of more than 95 per cent was maintained until 1946 and 1947 when there was a loss of approximately 5 per cent. Possibly the small losses in treatments C and D resulted from the unfavorable growing conditions in 1946. The loss in cover on A in 1945 was due mostly to the accidental fire previously referred to. Only in treatment E, was

TABLE II. *Average spring and fall basal cover of short grasses on each series of quadrats in each square*

Year	A	B	C	D	E	F	G	H	I	J	K	L
1942	72.3	69.4	69.2	68.1	68.5	71.5	71.2	75.1	70.8	73.9	69.8	66.7
1943	97.0	97.0	96.6	94.2	95.5	93.3	97.9	96.4	95.8	96.9	94.5	93.9
1944	98.0	98.4	97.2	97.5	93.5	93.5	98.2	98.5	97.6	96.5	95.2	95.5
1945	92.9	96.5	97.7	96.9	93.8	97.0	96.7	97.9	97.9	96.3	93.3	92.5
1946	94.3	93.4	94.3	95.2	80.3	88.3	94.4	95.9	94.5	88.6	91.1	83.7
1947	92.1	87.4	90.1	88.6	74.0		98.6					
Avg.	91.1	90.2	90.9	90.1	84.3	84.6	92.9	92.6	91.3	90.5	86.4	86.5

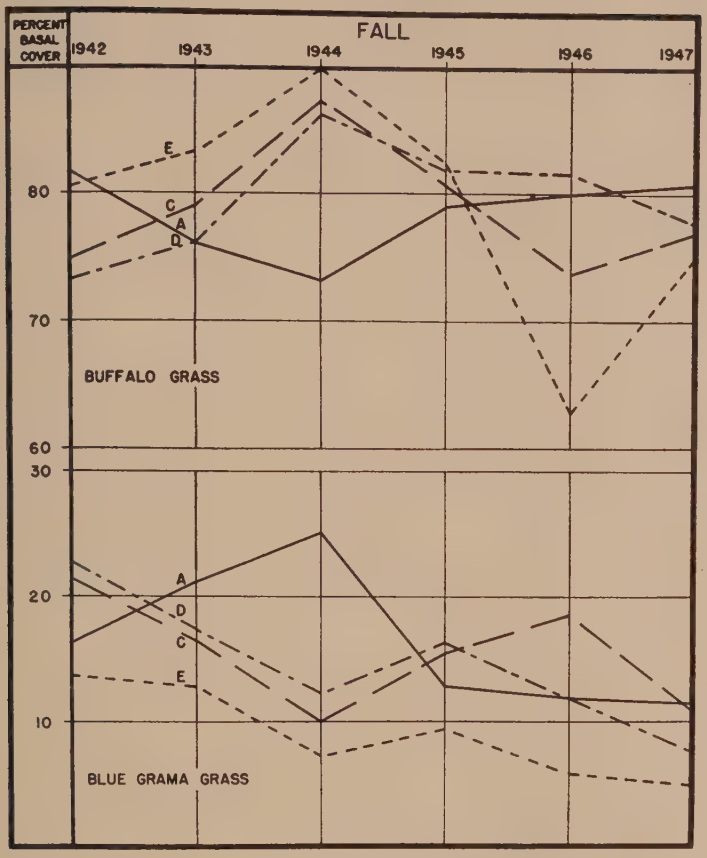

FIG. 5. Basal cover of buffalo grass and blue grama when unclipped (A), lightly clipped (C), moderately clipped (D), and closely clipped (E) for 1942–1947.

there any damage to cover due to clipping.

Averages of fall and spring cover on all areas used in the study are given in Table II. It will be noted that in treatments K and L, the most heavily clipped and deferred clipped areas, respectively, the reduction in cover was similar to that of E in the other series. Reduced cover resulted in considerable surface erosion. Soil washed from the closely clipped quadrats usually lodged in the border vegetation on the lower side of the quadrat.

When the quadrats were charted each fall, separation was made between cover of blue grama and buffalo grass (Fig. 5). It seems significant that on A, the unclipped area, the cover of buffalo grass decreased during the first three years, while in the same period blue grama made a steady gain. Furthermore, during the last three years the cover of buffalo grass increased and that of blue grama declined.

Decrease in cover of blue grama in 1945, where debris was heavy, was due mostly to the fire. Buffalo grass on C and D gained in cover until 1944, after which there was a gradual decrease. Buffalo grass on E also gained until 1944, after which the loss was severe. A low of 62 per cent was reached in 1946. In 1947, under more favorable conditions, the cover of 1945 was nearly restored. It seems from these data that buffalo grass withstood heavy clipping more successfully than did blue grama,

especially during the first three years of study.

Yield

Yield throughout the study tended to follow the summer rainfall curve except that heavy clipping made drought more effective in reducing yield and limited considerably the beneficial effects of bountiful rainfall (Fig. 6). Yield, where not influenced by clipping, was approximately 100 pounds per acre for each inch of summer rainfall. After two years of close clipping, however, the amount was reduced nearly 50 per cent.

During the first year, yield was significantly greater on the closely clipped areas than it was on those more lightly clipped or unclipped. This was probably due to clipping stimulus and was made possible by using food reserves for extra growth. In 1943, when summer rainfall was unusually low, yield on all areas was between 1,000 and 1,500 pounds per acre, which

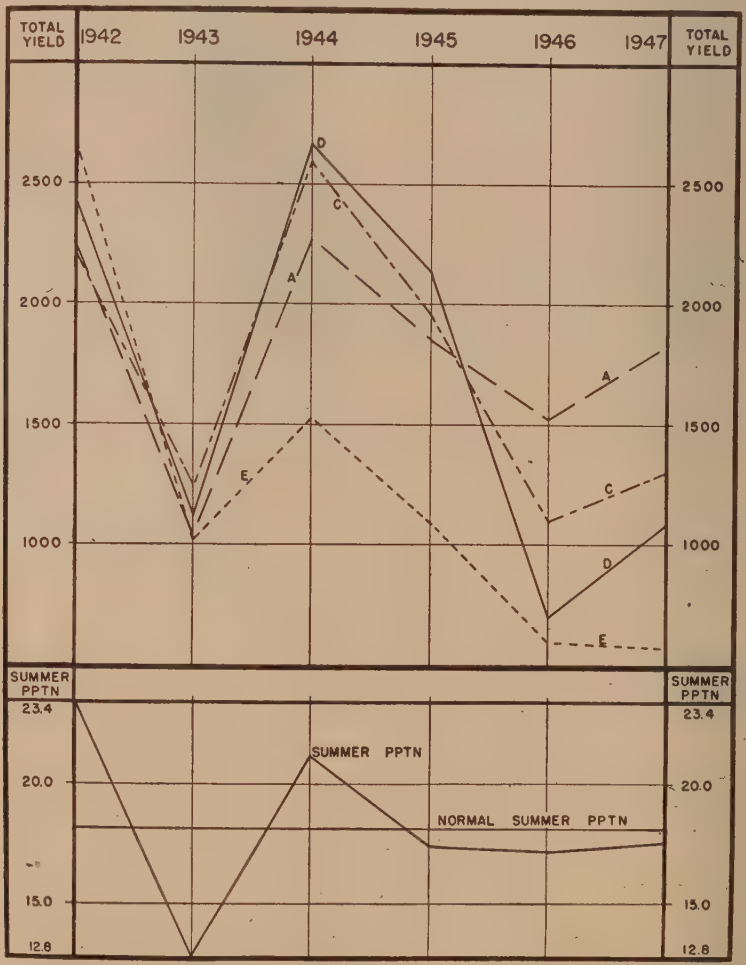

FIG. 6. Yield of short grasses from 1942–1947 when unclipped (A), lightly clipped (C), moderately clipped (D), and closely clipped (E). Also summer precipitation (pptn) for same period.

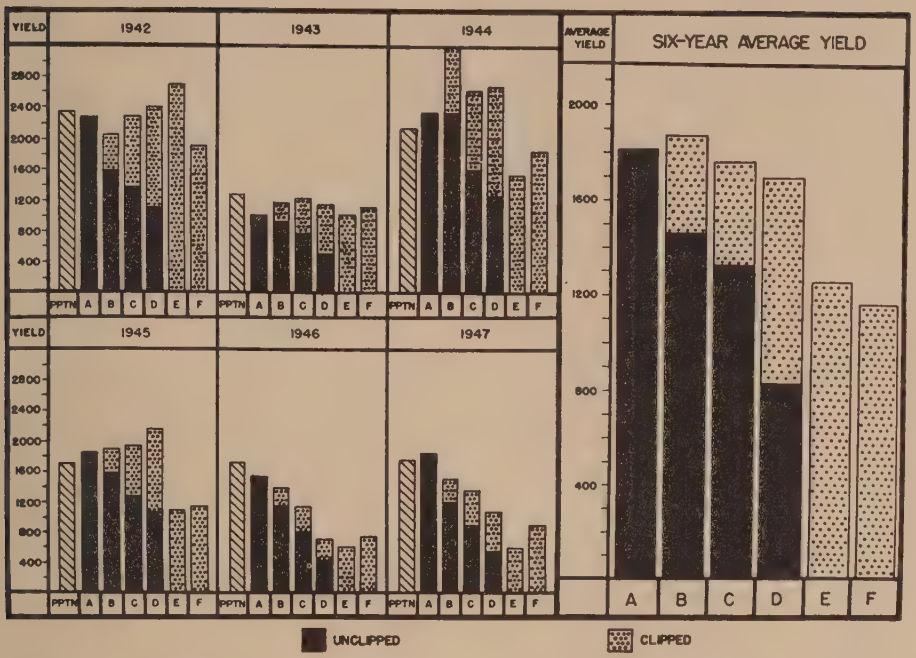

FIG. 7. Total yield and amount unclipped (black) and clipped (dots) of short grasses for each year and six-year average on one series of six treatments. Precipitation (pptn) for season (April to September) is also given.

was less than half the yield during 1942. There seemed to be no significant effect of intensity of clipping on yield during this season. After the second year, however, the detrimental effects of heavy clipping became apparent. Yield during the wet season of 1944 was higher than in all other years on all areas except those most heavily clipped. Treatment E produced only 1,500 pounds per acre in this year and decreased rapidly thereafter. All yields decreased during 1945 and 1946, when summer rainfall was below normal. This was particularly true in 1946 when rainfall was not only low but, as indicated earlier, it was also poorly distributed through the growing period. There was increased yield in 1947 on all areas except those closely clipped where there was a slight reduction. It is noteworthy that in 1942 yield on the closely clipped areas was over 2,700 pounds per acre—nearly 500 pounds greater than on ligthly clipped and unclipped areas. In 1947, however, yield on the closely clipped areas was only 588 pounds per acre in comparison to 1,800 pounds on unclipped areas.

Yield on the second series (treatments G, I, J, and K) ran nearly parallel to those of treatments A, C, D, and E, except that on K, the most heavily clipped area, detrimental effect of heavy clipping appeared in 1943 instead of 1944. The two most heavily clipped areas, J and K, were lowest in yield from 1944 to 1946 inclusive. No yields on these areas were secured in 1947 because of disturbance due to root studies.

Total yield and amount harvested on all areas in treatments A to F are given in Figure 7. It was obvious that clipping stimulus first appeared on E where nearly all vegetation was removed every two weeks. The detrimental effect of heavy clipping appeared in the second year but lighter clipping continued as a stimulant to growth for two more years. During

TABLE III. *Per cent of total yield and inches of seasonal rainfall (Rf) before and after July 1*

Year	C		D		E	
	Before July 1	After July 1	Before July 1	After July 1	Before July 1	After July 1
Rf 1942	16.70 62.6	6.72 37.4	50.5	49.5	57.6	42.4
Rf 1943	4.98 74.7	7.84 25.3	66.5	33.5	54.0	46.0
Rf 1944	8.56 61.1	12.65 38.9	49.7	50.3	53.7	46.3
Rf 1945	12.70 60.7	4.76 39.3	78.4	21.6	70.2	29.8
Rf 1946	8.55 75.6	8.83 24.4	74.9	25.1	84.0	16.0
Rf 1947	14.51 80.0	3.01 20.0	72.3	27.7	80.0	20.0

1946 and 1947, however, total yield decreased with intensity of clipping from A, the unclipped area, to E.

Yield on treatment F, deferred until July 31, was usually significantly less than on all other areas except E. Average yields for the six-year period indicated that no great amount of clipping damage occurred on any areas except E and F.

Yield before and after July 1

Much interest has been shown in time of season when growth occurs. Records were kept on weights of clippings made at various intervals. These weights were combined to give amount of forage produced before and after July 1 of each year. Per cent of total yield that occurred before and after July 1 on light (C), moderate (D), and heavy (E) clipping are given in Table III. Inches of rainfall before July 1 (April, May, and June) and after July 1 (July, August, and September), are also given.

During 1942, with available soil moisture throughout the season, nearly 63 per cent of the harvested forage was produced before July 1 on C. Amount on D was only slightly more than half (50.5 per cent) the season's harvest, but on E, where clipping was heavy, 57.6 per cent was harvested before July 1.

During the dry season of 1943, response to clipping was significant on closely clipped areas. Here the relatively short blades of grass remained green and continued to grow through much of late summer and, as a result, only 54 per cent of the harvest occurred before July 1. On C and D, however, percentage produced before July was 74.7 and 66.5, respectively. This is considerably more than in 1942. In 1944, amounts harvested before and after July 1 were nearly the same as those of 1942.

For the years 1945, 1946, and 1947, percentages harvested before July 1 generally were greater than during the first three years of study. This was especially true for D and E. In fact, on E only 16 and 20 per cent was produced after July 1 in 1946 and 1947, respectively. It seemed evident that effect of close clipping on E (and fall drought in 1947) reduced the vigor of the grasses to the extent that most was produced before July 1.

Protein content

Samples from different treatments were analyzed to find effect of various intensities of clipping on protein content. During the first half of June, 1942, protein content of the short grasses (blue grama and buffalo grass) was 11.97 per cent on treatment C, the lightly clipped area. On E, the closely clipped area, it was 13.53 per cent. During the first half of July, however, per cent protein was 9.56 and 13.37, respectively, on treatments C and E. One month later amount of protein in C had decreased to 9.02 per cent, but on E it was 14.57. In September, however, percentage of protein had increased slightly to 9.17 per cent in C, but on E it had dropped to only 13.62. By the middle of October the amount had decreased to less than 7 per cent on both areas.

At the close of study in 1947, per cent protein during early July was 10.73 and 12.2, respectively, in treatments C and E. In early July when soil moisture was

FIG. 8. Broken cover with considerable erosion after five years of close clipping.

abundant from nearly 7 inches of rainfall in June, amount of protein in both treatments was over 12 per cent. In August, however, following considerable drought, clippings made on C contained 10.67 per cent, while on E it was 13.85. No attempt was made to determine in detail the protein content of the vegetation throughout the study but only to discover if the green growth on heavily clipped areas

FIG. 9. Cover remained unbroken where clipping was moderate.

maintained a higher protein content than did vegetation on the lightly clipped areas.

Other effects of clipping

At the close of study there was a vast difference in general appearance of vegetation in various treatments. On unclipped areas, old vegetation had gradually accumulated, and renewed growth in spring was somewhat delayed. Open spaces between tufts of grass were so thoroughly filled with old debris that it was difficult to chart cover accurately. Total number of weeds was considerably less here than on those areas where some of the vegetation was removed. Little barley was the most common weed found in the unclipped areas, whereas, broad-leaved invaders were more numerous on all clipped areas and particularly on those closely clipped. Most common of the weedy broad-leaved plants on clipped areas were muletail (*Erigeron canadensis* L.), Venus looking glass (*Specularia perfoliata* (L.) A.D.C.), whitlowgrass (*Draba caroliniana* Walt.), stick tight (*Lappula* spp.), plantain (*Plantago* spp.), peppergrass (*Lepidium densiflorum* Schrad.), and tansy mustard (*Sophia* spp.). Six-weeks fescue was also common in open spaces.

On closely clipped areas there was no accumulation of debris, and as open spaces became larger, washing of soil from runoff water became conspicuous (Fig. 8). It was not uncommon to find as much as .5 or .75 inch of soil washed away from the open spaces, often 8 inches across, leaving tufts of grass on little mounds. Growth of vegetation in lanes near the closely clipped areas was usually greater than farther away where there was no border effect. Moderately clipped areas showed no signs of erosion (Fig. 9).

Number of roots in 4-inch circles was determined at the end of the first season in 1942. Similar counts were again made in the fall of 1945 and at the close of the study in the fall of 1947. In 1942, number of roots at the upper levels of soil were consistently greater on heavily clipped areas (E) than where moderately clipped

FIG. 10. Roots of grass from columns of sod twelve inches square after five years of clipping to stimulate non-grazed (A), moderately grazed (D), and heavily grazed (E).

(D) or unclipped (A). For example, there were 141 roots in 4-inch depths in E, 131 in D, and 107 in A. The difference was similar at depths of 8 inches and 12 inches, but from depths of 48 inches to 60 inches there was a reversal in number and generally most roots were found in the moderately clipped areas. After 4 years of clipping, numbers of roots at the 4-inch depth were 107, 299, 212, on E. D. and A, respectively. It should be noted that the number of roots had increased in treatment A and D but decreased in E in com-

parison to 1942. In the fall of 1947, number of roots at 4-inch intervals was always greatest in the moderately clipped area. Next highest was in the unclipped areas. The number in the heavily clipped areas was significantly less than in others in all depths.

Weights of roots in 4-inch layers, 100 square inches in area, were also determined in the fall of 1947. In most cases, the weight in the unclipped area was considerably greater than in either of the other areas. For example, there were 33.3 grams in the top 4-inch layer in treatment A, 23.1 grams in D, and 21.7 grams in E. In the layer from 16 to 20 inches in depth, the weights of roots in A, D, and E, respectively, were 3.3, 2.7, and 1.4 grams. In the 44 to 48 inch layer the weights in the above order were 1.3, 1.1, and .6 grams; and at six feet, .11, .10, and .03 grams. Weights of roots in 100 square-inch sods to the full depth of 84 inches were 90 grams in A, 60 grams in D, and 40 grams in E.

After 5 years of study, sods one foot square and 6 feet deep were removed from treatments A, D, and E. Soil was washed from the roots to determine amount and depth of roots (Fig. 10). No significant differences were apparent in A and D, but in E there was considerable decrease in both amount of roots and depth of penetration.

Recovery

After five years of removal of vegetation, clipping was discontinued on a portion of the area and measurements of recovery were begun. It was found that at the close of the first season after clipping was discontinued, an average maximum height of 9.9 inches was produced by buffalo grass on the unclipped area. Increment was 6.9 inches on the lightly clipped area and only 4.4 inches on locations where complete removal was made each week. Blue grama suffered fully as much as did buffalo grass. On the ungrazed area, blue grama attained a foliage height of 11.2 inches and flower stalks were 15.6 inches in height. Length of foliage on the moderately clipped area averaged 5.7 inches and flower stalks 11.5 inches. On the heavily clipped area, however, no flower stalks were produced and foliage grew to a height of only 4.9 inches.

Recovery in 1948 on areas that were clipped through 1947, was similar to recovery in 1947 on areas last clipped in 1946. Total increment on unclipped areas at the close of the season was about 8.5 inches for both short grasses. Flower stalks on blue grama averaged 15–18 inches in height. On closely clipped areas, however, length of foliage was about 3.5 inches with a few scattered flower stalks reaching a height of 12.5 inches. Where intermediate clipping was practiced length of blades was 7–8 inches, and flower stalks on the blue grama reached a height of 17 inches. Where clipping was deferred until August 1 the blades reached a length of 6–7 inches and scattered flower stalks on blue grama were 14–15 inches in height.

Study was concluded in the fall of 1950 after three years of recovery. At this time it was still easy to distinguish the closely clipped grasses from surrounding vegetation. Blades on these areas were both shorter and fewer per unit area than on lightly clipped or unclipped areas. Buffalo grass on unclipped areas attained a height of at least 6 inches but it was nearly one inch less on those heavily clipped. Average height of blue grama blades was about one inch greater than on buffalo grass, but the same difference between unclipped and clipped was maintained.

Lack of complete recovery was also reflected in yield. Clippings made in November, 1950, indicated that yield on areas previously unclipped was about 2,700 pounds per acre, whereas it was less than 2,250 pounds per acre on areas that had been closely clipped from 1942–1947.

Discussion

The purpose of this study was to determine response of blue grama and buffalo grass to various degrees of use over a comparatively long period of time. Clipping

to stimulate different intensities of utilization was continued for six years and it early became evident that close clipping and deficient soil moisture together had a pronounced effect upon behavior of the two short grasses studied.

Early in the study, growth was greatly stimulated by close clipping. Later, however, this type of use had so weakened the grasses that growth was significantly decreased, especially during seasons of deficient soil moisture.

Increment of top growth was greatest in all treatments under high summer rainfall. During the first season of clipping, it was nearly 20 inches on closely clipped areas, 12.3 inches under moderate clipping, and 7 inches on unclipped areas. Excessive growth evidently decreased food reserves in roots and crowns of closely clipped plants as indicated by the fact that after the second year of study, increment of top growth was least where clipping was most intense. Reduction in increment due to clipping appeared much later on moderately clipped areas.

Blades of grass became definitely lighter in color, shorter in length, and more sparse and slender under close clipping. Even the flower stalks on both species of grass were shortest and most slender on closely clipped areas. It was significant, however, that closely clipped grasses remained green, succulent, and high in protein in comparison to lightly clipped or unclipped grasses. As study progressed, many larger crowns began to deteriorate near the center. Even where living tissue remained, tillers were more sparsely distributed than on less closely clipped crowns.

Blue grama showed signs of clipping damage somewhat earlier than did buffalo grass. This was probably due to larger percentage of basal leaf surface on the latter species of grass. Stolons of buffalo grass, however, showed signs of clipping damage after two years of study and the effect was significant after 5 years when on June 1 the stolons were 10 inches long on the unclipped plants but only 2 inches long where close clipping had been followed. Open spaces in the vegetation resulting from death of crowns were usually occupied by annual weeds especially during years with moist soil in early season.

The crowns of grass that persisted were left on mounds 1 inch high where soil had been washed from open spaces after annual weeds had been removed or had died.

It was apparent that, during drought, the long, unclipped blades of grass died back from the tips to a much greater extent that was common on clipped grasses.

No significant reduction in cover occurred except on closely clipped areas. Yield, however, suffered greatly after the first year especially when clipping was close and frequent. Continued growth and high protein content were perhaps the only redeeming features of close clipping and these in time were offset by decrease in total yield.

At first the yield, like increment of top growth, was increased only to be followed by serious reduction as the food reserves became depleted. There was some evidence that both yield and increment suffered a greater decrease under close clipping when soil moisture was deficient.

Time of season when yield occurred was studied and summarized under percentage of total yield before and after July 1. It was evident that close clipping stimulated season-long growth during early years of study but in later years most growth occurred in springtime. Another factor that determined when growth occurred was time and amount of rainfall. During the dry summer of 1943, for example, much of the yield on light and moderate clipping occurred before July 1, but on closely clipped areas where food reserves were not yet depleted, growth continued well into late summer and only 54 per cent was produced before July 1. Generally growth was greatest when soil moisture was plentiful and least when soil moisture became deficient.

As clipping continued, food reserves evidently decreased and replacement of dead roots became impossible. Conse-

quently, at the close of study total amount of roots under close clipping was less than half the amount found under less intense treatments.

Recovery, after clipping was discontinued, was most rapid on lightly clipped areas. The weakened plants on closely clipped areas had not regained their original vigor when last studied in the fall of 1950 after 3 years of recovery.

It was found that after two years of study, yields were considerably reduced on areas where all vegetation was gradually removed after July 31. In fact, production on these deferred areas was very little more than on locations closely clipped each two weeks beginning May 25.

Grasslands came into existence through great adversity over long periods of time. They are hard to destroy unless put under cultivation. It is evident, however, that most of the yield (that portion that makes a profit for the rancher) is lost when use is too heavy to maintain a vigorous cover of native vegetation.

Summary

This study was conducted from 1942 to 1947 to determine the effect of various intensities of clipping on growth of blue grama and buffalo grass.

The experimental plot consisted of 2 square areas, each of which contained 36 one-meter quadrats. The quadrats in each area were arranged in 6 series, each of which consisted of 6 quadrats.

Each series was clipped at different intensities and different frequencies through the growing seasons. Amount of grasses not removed by clipping was determined by a utilization gauge or by clipping similar locations outside the areas of study.

Per cent basal cover of vegetation was determined each spring and fall by a pantograph and planimeter.

Soil moisture to a depth of 5 feet was determined each week from soil samples taken with a geotome. Amount of moisture above hygroscopic coefficient was considered available for plant growth.

In the fall of 1942, 1945, and 1947 columns of sod to depths of root penetration were removed from areas unclipped (A), moderately clipped (D), and closely clipped (E). Roots were washed from 4-inch layers of sods, counted and weighed.

Precipitation in 1942 and 1944 was over 29 inches and well distributed through the growing season. The supply of soil moisture, therefore, was nearly ideal for plant growth throughout these summers.

In 1943 total precipitation was only 16.2 inches and deficient soil moisture was common through most of the season in all but the top few inches of soil.

During early parts of 1945 and 1947 there was sufficient soil moisture for plant growth but later in each summer light droughts occurred. In 1946 unfavorable distribution of rainfall caused severe summer drought.

Clipping stimulated top growth, especially during early years of study. During the first season total elongation of tops was nearly 20 inches on closely clipped areas and only 7 inches on unclipped ones. Total growth of moderately clipped grasses was 12.3 inches.

During 1943, when soil moisture was nearly always deficient, total increment was nearly normal on unclipped areas but it was significantly less than in 1942 on all other locations.

Clipping stimulus was still apparent under light to moderate clipping during the wet season of 1944, but on closely clipped areas it had been greatly reduced.

After 1944 increment of top growth was always least when closely clipped, and in 1946 and 1947, total increment was inverse to intensity of clipping.

There was no great effect of top removal on basal cover except under close clipping. Here crowns died in the centers and marginal tillers were more slender and sparse than elsewhere.

As the crowns died open spaces became larger and surface erosion of soil was more serious. Near the end of study many half-dead crowns were left on mounds nearly 1 inch high.

Decreased cover and increment on closely clipped locations resulted in great reduction in yield late in the study.

Complete removal of top growth late in season caused nearly as much reduction in yield of forage as when clipping continued throughout the season.

Roots also were greatly affected by close clipping. Under close clipping amount of tops and roots suffered more than a 50 per cent reduction in weight in comparison to moderate and light clipping.

Recovery was slow following six years of close clipping. Total yield, height and density of grasses were less than normal even after three years of recovery.

The one redeeming feature of close clipping was in maintaining through most of the season a cover of green, succulent vegetation fairly high in protein.

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STUDIES FROM THE AUTOTREPHON, I. SOME POINTS IN GENERAL OPERATION AND MAINTENANCE

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The Autotrephon, described in Stanley, 1951, though very carefully designed, is somewhat complicated, and the experience of two years has shown that there are some points with respect to its operation and maintenance which should be placed on record.

Warm-chamber controls. The setting of the thermostat for the humidifier heater (Stanley 1951, TH-3, Fig. 11) is very important. If it does not cut in and out within about 0.1° C., of the warm-chamber temperature, quite pronounced surges will occur in the temperature of that chamber. These will show as rather regularly spaced spikes or peaks on the temperature record. Under dry room conditions, where humidification is frequent, these spikes may run together to form a saw-tooth record. Dirty contacts on the warm-chamber thermostat (*ibid.*, TH-1, Fig. 3) produce a very irregular variation in the temperature record.

When the heater of the warm chamber (*ibid.*, H, Fig. 3) operates, it causes a small rise of temperature (about 0.3° C.) in the air flowing down the lateral air-channels of the warm chamber. As the wet-bulb thermometer is set in this stream (*ibid.*, WBT, Fig. 3), readings should not be taken when the heater is operating. A neon pilot light should be wired in parallel with the heater to act as an indicator.

When running with the warm-chamber temperature very close to that of the surrounding room, it will be found that the chamber tends to control on the cooling system during the day, and on the heater at night. This produces a reiterated "step" effect on the record. This cannot be eliminated, but it can be minimized by making the differential on TH-1 as small as possible. The differential should be reduced to the point where the cooling system just fails to operate from the minute overshoot of the heating system. This will give a differential of perhaps 0.15 to 0.2° C.

The differential of the humidistat (*Ibid.*, Fig. 5) should not be set too fine, as the contact arm (*ibid.*, CA, Fig. 12) naturally has a rather large swing. Experience is the only guide, but the total gap between the contact arm and the fixed contacts can be about 1/32 in. If the apparatus is shut down, the tension on the hair-strand should be released by turning the adjusting nut AN (*ibid.*, Fig. 12) until the strand is limp. If this is not done, the hairs may break on a dry day. To prevent the hair-strand twisting when the adjusting nut is turned, a small cross-pin should be put through the rod R (*ibid.*, Fig. 12). This should be located just where the end of the dotted pointer touches the rod, R, in Figure 12. It can be installed by sweating a brass sleeve (1/16 O.D.) over R, and drilling through this assembly, and sweating in a ¾-in. length of piano wire. If this wire is held between finger and thumb of the left hand while AN is turned with the right, adjustments are readily made.

The end-clips of the hair-strand were not clearly shown in Stanley 1951, and one is therefore shown herewith as Figures 1A and 1B. The clip should be milled out of non-thermoplastic bakelite, and cannot be re-used. The hairs are ordinarily human hair. We have not found that blond hairs are essential. The hairs need only be washed with ether prior to use, to wash off grease. Any good grade celluloid cement will do for cementing the hairs into the clip, but it is important that they be stretched evenly before cementing. This may be done by cementing into one clip, threading through the holes of the second clip, and hanging

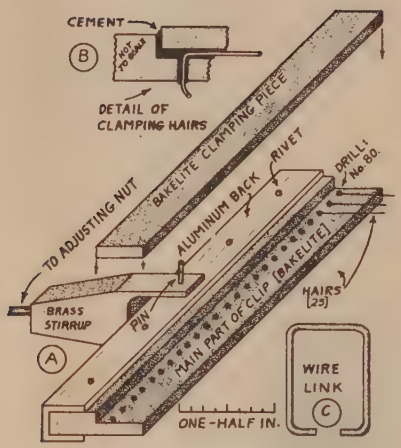

FIG. 1. Details of the construction of a hair-strand end-clip, and of a suitable form of wire link for linked tracking.

a split shot on each hair for an hour or two. The second clip is then cemented. It will be noted that the back of the clip is fastened to the operating rod by a simple pin, rather than by a ball-and-socket joint as mentioned in Stanley 1951, page 425. The original description was in error here.

The humidifier of the warm chamber (*ibid.*, p. 423 *et seq.*) should be cleaned out once or twice per year, as it collects much dust and flour. The de-humidifier has never been used in the McGill autotrephon. It seems certain that it is much too small as shown in Stanley 1951, Figure 11. It should hold enough silica gel to remove about 1 to 1.5 quarts of water per day if it is intended to operate at low humidities in a damp climate.

The heat exchanger. Evaporation of the water from the heat-exchanger water tank (*ibid.*, Fig. 9) may lower the water below the thermostat, resulting in a puzzling loss of control, or even freezing of the water. Such freezing would do irreparable damage. The exchanger at McGill seems to need re-filling about once in three months, and this job has therefore been put on the monthly maintenance sheet. A leak in the labyrinth is unlikely, and trivial if only small. A test can be made by adding a few drops of a solution of fluorescein to the tank water, subsequently testing the water in the humidifier with ultra-violet light. Any leaking water will pass to the humidifier through the dew drain-pipe (*ibid.*, p. 422). No attempt should be made to seal a leak by the use of any of the proprietory leak-stoppers used for automobile radiators. These will coat the labyrinth and interfere with cooling.

The tunnel. It has been found that when the cooling-blower of the cool storage chamber (*ibid.*, CB-3, Fig. 19) operates, it forces some air through the tunnel, past the doors, into the warm chamber. This does not seriously affect the temperature in the warm chamber, but it does chill the sample waiting at the escapement. This trouble can be cured by cutting a 2-in. hole through the floor of the tunnel. This will also prevent transfer of air from the warm chamber through the cool chamber to the main cooling coils, and it will not be necessary to defrost these coils so frequently. Defrosting is indicated when the cool chamber begins to warm above its proper temperature, and is needed about once per month. (See also under "Cool chamber.")

Should a sample stick in the tunnel, and get pinched in one of the doors, the enormous geared-up power of the door motor may damage the door-opening mechanism. To protect against this, the set-screw of the drive-plate (*ibid.*, DP, Figs. 17, 18) should be made of brass, with a flat tip, not dimpled into the shaft. This will slip under extreme torque.

Cool-storage chamber. A strip of suitably located sponge rubber should be cemented to the wall of the cool chamber on the side opposite to the entrance of the tunnel, to cushion the samples. These fly out by centrifugal force as they rush round the helix, and bash themselves on the wall. When defrosting the main cooling coils, the blower CB-3 of the cool chamber should be shut off, otherwise, there being no cooling available, it will run endlessly. It is also well to install mercury-tube switches on all chamber

doors and on the tunnel doors, to stop all blowers when doors are open. This saves loss and inter-chamber transfer of conditioned air.

Main cooling chamber. Much more efficient cooling will be obtained if all ducts blowing into the chamber have their inward ends poked into the interstices of the cooling coils. When the coil frosts, tunnels will be formed in the frost, and excellent cooling will result.

Ducting. Stainless steel flexible tubing should be used. Galvanized will rust and brass is corroded by the gas given off by *Tribolium* and by moisture which collects around small food particles which get blown into the ducts. The rubber-sleeve connections shown in Stanley 1951, Figure 7, are not too satisfactory. Well-made flanged connections with bolts and nuts would be much better.

Relays. The "Silent Power" relays used at McGill have proved excellent, but the clips holding the mercury tube must be screwed up *very* tightly, or the angle of inclination of the tube will change in time, and prevent proper operation of the controlled circuit.

Wire links for "linked" tracking. These have been quite troublesome. The design shown in Figure 1C of this paper is however, satisfactory. The links should be made of stainless steel spring-wire. The turned-in ends prevent the link pulling out of the anti-squeeze ring when a vial is tilted at the escapement as in the case of the lowest vial in Figure 3 of Stanley 1951.

When assembling a linked group, the links, the central plane of the group, and the plane between the rollers of each hanger should all line up. If this is not so, some vials may be slightly rotated with respect to the axis of the track, and the group will refuse to roll smoothly. This is a common cause of jamming in the escapement. It is well to oil the centre hole of each roller occasionally, with "Nujol." The track should be kept free from dust, and any corroded spots should be polished off.

Escapement. One should see that the set-screws locating the escapement lever (*ibid.*, LE, Fig. 13) and the two claws (CL-1 and CL-2, Fig. 13) are *very* tight. Use Allen socket-head set-screws with conical points. When only one or two vials are on the track, a few extra vials should be run down behind them as a make-weight, to assist them through the escapement. In setting the spread of the claws, see that when one of them touches the web of the track, the tip of the other is just level (in the claw-notch) with the side of the basal part of the escapement. There is thus nothing on which the rollers can catch as they go through. CL-2 is shown in the correct setting in Figure 13D of Stanley 1951.

The program controller. This is the source of the majority of failures in sampling. The bronze balls should be meticulously cleaned each time they are used, by some method which leaves no film of grease or wax on them. This can be done by wrapping a few of them in a cloth with a little "Bon Ami" (or other fine cleaning powder) and shaking them up for a few minutes. The dust should be blown off them before use. The cleaned balls should never be touched with the fingers. The magazine trough and the blades of the beak-switch (*ibid.*, Fig. 14) should be cleaned about once per week with "Bon Ami" on a pledget of cotton. A glass or plastic tube threaded over the magazine trough will keep out the dust, which can prevent rolling of the balls.

Much trouble has occurred with "double contacting" of the ball-hammer switch (*ibid.*, PCCS, PCI, PCCB, Fig. 14). This lets two balls go at one hour, and throws the whole subsequent program off time. This trouble was traced to wear of the centre bearing of the time-wheel, allowing it to tilt slightly as the contact fingers PCCS slide off the contact block PCCB. This establishes a momentary second contact, and flips an extra ball. The center bearing of the time-wheel should therefore be very care-

fully made, free from friction, shake or end-float.

Anyone making an autotrephon will hardly design the beak-switch exactly as the writer has done, but at all events, one should make sure that the insulating block of the moveable jaw (*ibid.*, PCMJ, Fig. 14) has a sloping top, sloped towards the opening of the switch. This prevents any small balls which may succeed in riding down one flange of the sieve rails, from roosting on top of this block. If they do this, they can cause a short circuit, opening the doors. Unless one knows of this, there can be some quite inexplicable ill-timed sampling operations.

General wiring. If trouble is to be avoided, this cannot be too well done. One should use heavy-gauge wire, insulated with "Flamenol," and all such units as motors, relays, etc., should be wired into the system via small terminal blocks such as those shown in Figure 10 of Stanley 1951. This allows a unit to be removed and replaced rapidly without unsoldering connections.

Practical programming. Stanley 1951, gave some details of programming as far as "tracking" is concerned, this being a term to denote the arrangement of balls in the controller magazine and of samples on the helix, required to realize a given sequence of sampling. Experience has shown that programming is something of a fine art, and some details of the accumulated knowledge follow.

If the programs are too full, an autotrephon can easily become a Frankenstein

TABLE I. *Portion of a program form, showing the initial set-up of the beginning of a typical program*

AUTOTREPHON PROGRAM

Run No. *17* **Start** *10 A.M. Monday, October 29*

Purpose *Intercomparison of Species (a, b, c, d), check samples of Species (e). Some odd samples of Species (f).*

Dry temp. ° C. *30* **Wet temp. ° C.** *26.4* **R.H.** *75%*

Heat exch. temp. ° C. *27* **Container** *Standard plastic*

Food medium *76-mesh flour, 3% germ, 30 gm.* **Eggs per sample** *25*

0					
1	25	49	73	97	121
2	26	50	74	98	122
3	27	51	*75 *f-1*	99	123
4	28	52	76	*100 *f-6*	124
5	29	53	77	101	125
6	30	54 *Sw. on*	78	102	126
7	31	55	79	103	127
8	32	56	*80 *f-2*	104	128
9	33	57	81	*105 *f-7*	129
10	34	58	82	106	130
11	35	59	83	107	131
12	36	60	*84 *e-1*	*108 *e-2*	*132 *e-3*
13	37	61	*85 *f-3*	109	133
14	38	62	86	*110 *f-8*	134
15	39	63	87	111	135
16	40	64	88	112	136
17	41	65	89	113	137
18	42	66	*90 *f-4*	114	138
19	43	67	*91 *f-5*	*115 *f-9*	139
20	44	68	92	116	140
21	45	*69	*93	*117	*141
22	46	*70	*94	*118	*142
23	47	*71	*95	*119	*143
24	48	*72 *abcd(1)*	*96 *abcd(2)*	*120 *abcd(3)*	*144 *abcd(4)*

TABLE II. *Sequence of events for part of the program shown in Table I*

Day	Date	Clock time	Sample no.	Serial Hour	Age Hour	Notes
Mon.	Oct. 29	10 A.M.		634	0	Start
Wed.	Oct. 31	4 P.M.		688	54	Switch-on
Thur.	Nov. 1	10 A.M.	abcd(1)	706	72	Linked quad
Thur.	Nov. 1	1 P.M.	f-1	709	75	
Thur.	Nov. 1	6 P.M.	f-2	714	80	
Thur.	Nov. 1	10 P.M.	e-1	718	84	
Thur.	Nov. 1	11 P.M.	f-3	719	85	
Fri.	Nov. 2	4 A.M.	f-4	724	90	
Fri.	Nov. 2	5 A.M.	f-5	725	95	Laid 4 hrs. early
Fri.	Nov. 2	10 A.M.	abcd(2)	730	96	Linked quad
Fri.	Nov. 2	2 P.M.	f-6	734	100	
Fri.	Nov. 2	7 P.M.	f-7	739	105	
Fri.	Nov. 2	10 P.M.	e-2	742	108	
Fri.	Nov. 2	12 Mid.	f-8	744	110	
Sat.	Nov. 3	5 A.M.	f-9	749	115	
Sat.	Nov. 3	10 A.M.	abcd(3)	754	120	Linked quad

Monster which overwhelms the staff. At the same time, one wishes to keep an expensive machine busy. The answer lies in skillful programming. Experience has shown that one trained worker can examine about 12 samples per day, and look after flour sifting and some record-keeping. With first-class programming, an autotrephon can keep two or three examiners busy, with some part-time help from a less well-trained person, making up diets. For a brief period, with one examiner, more than 12 samples per day can be run out, because they can stay in cool storage for as much as a week without undue desiccation, and one can catch up.

In making up a program, and arranging the necessary tracking, the writer begins with a mimeographed form listing the hours from 0 to 1,000. A part of such a form is shown in Table I. Without reference for the moment, to calendar or clock-times, and depending upon what is to be done, suitable numbered hours are marked for sampling (marked with an asterisk in Table I). As this is done, decisions are made as to the type of tracking which will take the samples out as required, without having conflicts at any hour, and so on. Links are denoted by underlines as shown at 72, 96, 120, and 144 hours in Table I. The hours at which the doors are to open are marked with an asterisk.

Table I shows linked tracking for quads of species (a, b, c, d) every 24 hours, with a fifth species (e) intercalated to sample every 24 hours, and a sixth species (f) intercalated to sample every 5 hours. It is seen that the 95-hour sample of Species (f) would interfere with the quad coming out at 96 hours. It is therefore prepared from eggs laid 4 hours earlier than the rest, and run out at 91 hours, when it is 95 hours old. Actually, this is not a very clever solution. It would be better to make the 96-hour quad into a quint, and accept a 1-hour delay in Sample f-5, or use "racked" tracking for the quad.

A suitable time for starting the run is then selected, say 10 A.M., Monday, October 29. From a table showing the serial numbers of each successive clock-hour from some suitable starting time (we use midnight, October 1), this starting time (on Monday, October 29) is found to be

TABLE III. *Ball-loading list for the specimen program shown in Tables I and II*

Switch on controller at 3:59:59 P.M., Wednesday, October 31

15S	3S	3S	1S	11S	8S
4L	2L	1L	1L	1L	4L
2S	4S	4S	4S	8S	11S
1L	2L	1L	1L	4L	1L
4S	1S	2S	1S	11S	8S
1L*	4L	1L	4L	1L	4L

* Read successively down the columns.

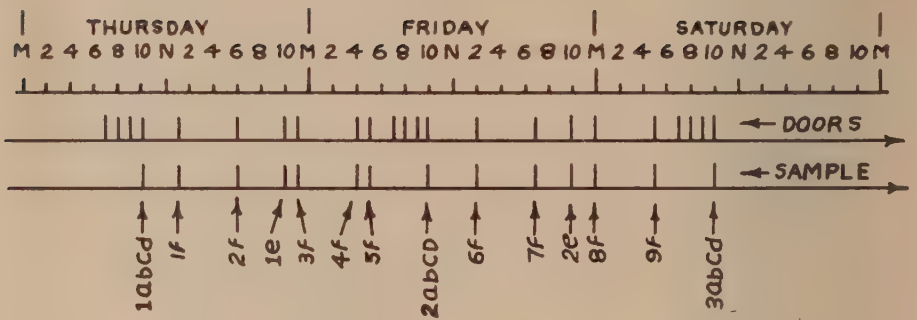

FIG. 2. Diagrammatic presentation of the record made by the checking system of the autotrephon for the specimen program of Table II. A diagram had to be used because the actual recording is very small, and difficult to photograph.

Serial Hour 634, and is Age Hour Zero of Table I.

A convenient time for switching on the controller must then be selected, as this determines the first part of the controller ball-loading. It will be seen from Table I that the first door-opening (to begin getting out the 72-hour quad) is at Age Hour 69, which is Serial Hour 634 plus 69, or 703. From the Serial Hour list, this is found to be 7 A.M. Thursday, November 1, so that a convenient time to switch on would be during the previous afternoon, say at 4 P.M., Wednesday, October 31. This is Serial Hour 688 and Age Hour 54. The initial loading of small balls to carry the controller from Serial Hour 688 to Serial Hour 702 inclusive (the last hour with a small ball, before 703 which uses a large ball) is 15 small balls, followed by 4 large, 2 small, etc., etc., as in Table III.

By a continued use of the Serial Hour table and a calendar, the dates and times (clock) of all the sample-withdrawals are determined and a list of the sequence of events is drawn up as in Table II. A ball-loading list is drawn up as in Table III, and the controller is loaded by reference to this list.

The record of what actually happens is made by the checking system (*ibid.*, p. 440) and for the program used here as an example, would appear diagrammatically as in Figure 2. If the reader will check this figure against Table II, he will see that the two are the same.

Reversed tracking. Since the original description of the autotrephon was written, the problem has arisen of setting up runs with insects such as *Oryzaephilus*, which do not readily produce the huge mass-cultures so easy to obtain with *Tribolium*. In such cases, one cannot get enough eggs all within plus or minus 1 hr. of the same age, to set up all the samples at one time. If one builds up one or two samples each day, and tracks forward in the usual way, the time required for a run is at least twice the life-history time. The method of reversed tracking ameliorates this difficulty.

Using this method (which was worked out by the writer's Research Assistant, Miss Helen J. Martin), the samples made up early are set aside to mature, and subsequently taken out as the older samples, and the samples made up on each successive day are used for successively younger points in the life history. Theoretically, if samples are made up every 12 hours (say) and sampling is done by the autotrephon every 12 hours, all the samples will come out at the same time, but by a little skill in programming, matters can be so arranged that one obtains a sequence of samples of various ages, spread over a few days as to time of withdrawal from the warm chamber. With this method, the time required for a run is only

a few days more than the life-history, and one can work from small egg-farms.

Setting up the samples for a run. It is to be emphasized that the autotrephon will not produce the high-grade data which it is capable of giving unless the technique is meticulous. This laboratory uses the following scheme for setting up the samples.

A few days before the selected time of starting the run, sufficient sample-vials are washed, dried and labelled with the sample numbers, and the required food is weighed into them. This food will have been kept under the required controlled conditions for some days, to come into equilibrium with these conditions. The filled vials are then set in a controlled chamber, to remain in equilibrium.

The "egg-farm" or culture is sifted clear of eggs one hour before the starting time, and one hour after it. The eggs collected in the two-hour period are carefully cleaned of all intermixed frass and food particles by the method of Stanley 1941, p. 25. These eggs will then have an age-spread of plus or minus one hour around the starting time. If very large cultures are available, the spread can be reduced to plus or minus ½ hour.

One has now about 72 hours before any hatching occurs, in which time one counts out the egg-batches and seeds the samples. The eggs, carefully kept under controlled conditions, are taken out in small batches and counted into open-topped shell-vials using the egg-counter of Stanley 1941. The vials are labelled like the sample-vials and returned as soon as possible to controlled storage. When all batches have been counted out, the sample-vials are laid out on a long bench in the order of the program, each with its egg-vial beside it. The anti-squeeze rings are put on, and lids and necessary links put beside the vials.

Two or three experienced people then begin tipping the eggs into the sample-vials, stirring them in with a probe. If the experiment is such that cannibalism is a problem, the flour and eggs in each sample-vial are thoroughly shaken in a flask. After a check to see that all egg-vials are empty, the sample-vials are shaken side-ways to level the flour and bumped once on the table to settle it. If the experiments are for any sort of critical population growth study, we use a standard bump on a slab of slate covered with heavy paper. After this the lids are added, linked groups assembled, and all but 72 sample-vials or fewer replaced in controlled storage. The 72 or fewer are put on the warm-chamber helix.

Single vials can be loaded onto the helix by holding in the right hand, splitting the pair of rollers of the hanger apart with the nail of the left thumb and threading over the web of the track. If the web is sharpened to an edge at the end, this is easier to do. A quad is too large to hold, and should be held in a small box, like a bricklayer's hod. One should watch the vials race down the helix, which they should do with a hearty accelerating rush. If they lag, there is a dirty roller or crooked link. This should be attended to, or the sample may stick in the escapement.

Summary

Details are given as to sundry points which have arisen in the operation and maintenance of the McGill Autotrephon, briefly as follows:

1. The humidifier heater thermostat should be set exactly at the warm chamber temperature.

2. The wet-bulb temperature of the warm chamber should not be read while the warm chamber heater is running.

3. When operating close to room temperature, the warm chamber controls by day on its cooler and by night on its heater. The resultant slight variation in controlled temperature can be minimized, but not eliminated, by reducing the differential of the thermostat.

4. The hair-strand of the humidistat should be relaxed (to prevent snapping the hairs) when the apparatus is shut off.

5. Details are given of the hair-strand end-clip, and of the making of a strand.

6. The humidifier should be cleaned once or twice per year. The de-humidifier, not used at McGill, is almost certainly too small.

7. Evaporation losses from the water-tank of the heat exchanger may lower the water below the thermostat (in about 3 months). This will ruin control. Leaks in the labyrinth can be detected by testing the water in the humidifier, to which leaking water will drain. Use a fluorescent indicator. Do not use leak-stopping compounds to mend leaks.

8. A 2-in. hole in the floor of the tunnel prevents air transfer between the warm and cool chambers, and *vice versa*.

9. A brass set-screw in the drive plate of the door-opening mechanism will slip under torque if the doors jam on a sample, and protect the mechanism.

10. A rubber buffer-strip cemented to the wall of the cool chamber will protect samples which bang the wall as they run down the helix.

11. Cut-off switches are desirable on all doors (chambers and tunnel), to cut the blowers when any doors are open.

12. Ducts blowing into the cool chamber should be poked into the cooling coils, for greater efficiency of cooling.

13. Ducts should be of stainless steel. Galvanized will rust, and brass will corrode.

14. Tube-clips of relays should be screwed up very tightly, or the tubes will shift, and fail to function.

15. A design is shown for wire-links (for linked tracking), with turned-in ends, which catch on the anti-squeeze rings, and thus prevent links coming undone.

16. Escapement claws and the escapement lever should be fastened very tightly with pointed set-screws. Claws should be carefully set as per Figure 13 of Stanley 1951.

17. The balls of the program controller should be cleaned each time they are used by rubbing in a cloth with "Bon Ami," and the beak-switch and magazine trough should be occasionally cleaned in the same way.

18. The bearing of the time-wheel should be smooth-running, but free from all play or shake, or extra contacts will occur at the hammer switch, spilling extra balls, and spoiling the program.

19. The beak-switch should be so made that any small balls which accidentally reach it, cannot catch in it, and produce false sampling.

20. Wiring throughout should be of heavy-gauge, "Flamenol" insulated, with all units connected through small terminal boards, for quick removal and replacement in servicing.

21. Details are given of practical programming, showing suitable forms which assist in making up a program.

22. A type of "reversed tracking" is described, suitable for dealing with insects which cannot be obtained in large cultures. In this method, the samples made up first are used for the older observations, and *vice versa*.

23. A description is given of the setting-up of the samples for a run.

References

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STUDIES FROM THE AUTOTREPHON, II. THE ANALYSIS OF AUTOTREPHON DATA

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INTRODUCTION

The traditional way of determining life histories of insects is to obtain a batch of eggs and rear as many as will survive to maturity, making observations meanwhile on hatching, ecdysis, pupation and emergence, *using the same material* throughout the series of observations. This method has the advantage of low variance if a single large batch of eggs can be obtained initially. There is also continuous knowledge of mortality rates from instar to instar. The disadvantage lies in the difficulty of making sufficient observations to obtain a coherent and detailed narrative. The method is also characterized by the fact that the numbers of survivors always *decrease* and *never* increase.

Using an autotrephon (Stanley 1951) however, one commences with enough eggs to provide a suitable seeding for each of numerous replicated samples, uses one sample for each observation, and then discards because the sample is ruined for further growth by the cool storage. Observations can be taken continuously, day and night, at intervals of as little as one hour, but it has been found that once every 5 to 10 hours is often enough. The all-over variance is greater from observation to observation because one is using a new sub-batch for each observation. In contrast to the traditional method, survival does not decline smoothly, but shows a random variation superimposed on a general (and sometimes hidden) downward trend. This trend must be unearthed statistically, and this may be impossible if the slope is extremely small. One can often have more survivors in one observation than in the previous one. It is obvious then, that one must have a special method for the analysis of autotrephon life-history data.

There follows a description of a single run on the life-history of *Tribolium confusum* Duv., showing how the analysis is carried out. Of set purpose, the discussion is restricted to this single run, in order to keep the discussion brief and clear. This will clear the way for further papers on *Tribolium* and other stored-products insects, which papers are in course of preparation at the time of writing.

DISCUSSION

In an ordinary life-history run, not complicated by any special features, the data will appear much as in Table I, and as plotted in the raw in Figure 1. These data are for a run with the McGill strain of the ordinary "red" variety of *Tribolium confusum,* the insects being lineal descendants of Chapman's (1934) culture at the University of Minnesota. The temperature was $30 \pm 0.15°$ C., and the Relative Humidity $75 \pm 2\%$. The samples consisted of 32 gm. of the writer's special flour; this is sifted whole wheat (Ogilvie "C"-stream, unbleached) flour plus 3% of ground wheat germ as described in Stanley, 1938), each sample seeded with 25 eggs. The eggs had a total age-spread of plus or minus 1 hr. around the median time of laying. The containers were the standard plastic of Stanley, 1951. Samples were taken (in theory) every 5 hours but there are some variations from this. A few extra samples were intercalated for better discrimination, and a few were missed (155, 160, 475 hrs.) due to what the radio announcers call "circumstances beyond our control" which means that the autotrephon did not work properly at these hours.

TABLE I. *Numbers and percentages of various life-history stages present in the samples drawn on one run of* Tribolium confusum *at 30° C., and 75% R.H. Initial seeding of eggs: 25 per sample, in 32 gm. of flour. Italic figures are percentages of total present*

Sample number	Time, hours	Eggs	Larval instars						Pupae	Adults	Total
			1	2	3	4	5	6			
1	90	25 *100*									25
2	95	25 *100*									25
3	100	25 *100*									25
4	105	25 *100*									25
5	110	25 *100*									25
6	115	15 *62.5*	9 *37.5*								24
7	120	11 *44.0*	14 *66.0*								25
8	125	7 *28.0*	18 *72.0*								25
9	130	7 *29.2*	17 *71.9*								24
10	140	5 *23.8*	15 *71.4*	1 *4.8*							21[1]
11	143	2 *10.5*	11 *57.9*	6 *31.6*							19
12	146	1 *5.6*	7 *38.9*	10 *55.6*							18
13	149	5 *21.7*	7 *30.4*	11 *47.8*							23
14	152	1 *5.0*	5 *25.0*	14 *70.0*							20
15	155										1
16	160										1
17	165			15 *100*							15
18	170			17 *100*							17
19	175			14 *100*							14
20	180			18 *100*							18
21	185			15 *100*							15

TABLE I—*Continued*

Sample number	Time, hours	Eggs	Larval instars						Pupae	Adults	Total
			1	2	3	4	5	6			
22	191			15 *100*							15
23	191			13 *100*							13[2]
24	195			15 *100*							15
25	200			14 *100*							14
26	205			20 *100*							20
27	210			18 *100*							18
28	215			19 *100*							19
29	218			12 *85.7*	2 *14.3*						14[3]
30	221			10 *62.5*	6 *37.5*						16
31	224			11 *68.7*	5 *31.3*						16
32	227			4 *28.7*	10 *71.4*						14
33	230			3 *15.0*	17 *85.0*						20
34	233			5 *27.8*	13 *72.2*						18
35	236				18 *100*						18
36	240			1 *5.6*	17 *94.4*						18
37	245			2 *5.6*	16 *94.4*						18
38	250				13 *100*						13
39	255			1 *5.9*	16 *94.1*						17
40	260			1 *5.9*	16 *94.1*						17
41	265				19 *100*						19
42	270				18 *100*						18
43	275				15 *100*	1 *6.2*					16

TABLE I—*Continued*

Sample number	Time, hours	Eggs	Larval instars						Pupae	Adults	Total
			1	2	3	4	5	6			
44	280				11 *68.7*	5 *31.3*					16
45	285				8 *44.4*	10 *55.6*					18
46	290				9 *45.0*	11 *55.0*					20
47	295				5 *33.3*	10 *66.7*					15
48	300					16 *100*					16
49	305					18 *100*					18
50	308					20 *100*					20[4]
51	311				1 *5.3*	18 *94.7*					19
52	314					17 *100*					17
53	317					18 *100*					18
54	320					16 *100*					16
55	323					15 *100*					15
56	326					19 *100*					19
57	329					13 *100*					13
58	332				2 *13.3*	12 *80.0*	1 *6.6*				15
59	335					16 *88.9*	2 *11.1*				18
60	340					13 *68.4*	6 *31.6*				19
61	345					6 *54.5*	5 *45.4*				11
62	350					4 *26.7*	11 *73.3*				15
63	355					3 *18.8*	13 *81.2*				16
64	360					1 *6.6*	14 *93.3*				15

TABLE I—*Continued*

Sample number	Time, hours	Eggs	Larval instars						Pupae	Adults	Total
			1	2	3	4	5	6			
65	365						18 *100*				18
66	370					1 *5.6*	17 *94.4*				18
67	375						18 *100*				18
68	380						18 *100*				18
69	385						16 *100*				16
70	390						18 *100*				18
71	395						19 *100*				19
72	400						18 *90.0*	2 *10.0*			20
73	405						13 *72.2*	5 *27.8*			18
74	410						12 *57.1*	9 *42.2*			21
75	415						5 *25.0*	15 *75.0*			20
76	420						1 *6.2*	15 *93.7*			16
77	425							20 *100*			20
78	430						1 *6.2*	15 *93.7*			16
79	435							16 *100*			16
80	440						1 *5.9*	16 *94.1*			17
81	445							19 *100*			19
82	450						1 *5.6*	17 *94.4*			18
83	455						1 *5.3*	18 *94.7*			19
84	460							18 *100*			18
85	465							15 *100*			15
86	470							16 *100*			16

TABLE I—*Continued*

Sample number	Time, hours	Eggs	Larval instars						Pupae	Adults	Total
			1	2	3	4	5	6			
87	475										[6]
88	480							16 *100*			16
89	485							22 *100*			22
90	490							16 *100*			16
91	495							18 *100*			18
92	500							19 *100*			19
93	505							18 *100*			18
94	510							18 *94.7*	1 *5.3*		19[6]
95	515							17 *100*			17
96	520							13 *76.5*	4 *23.5*		17
97	525							5 *31.3*	11 *68.7*		16
98	530							7 *43.8*	9 *56.2*		16
99	535							5 *31.2*	11 *68.8*		16
100	540							2 *18.2*	9 *81.8*		11
101	545							9 *45.0*	11 *55.0*		20
102	550							1 *7.1*	13 *92.9*		14
103	555							2 *11.1*	16 *88.9*		18
104	560							2 *10.0*	18 *90.0*		20
105	565								20 *100*		20
106	570								20 *100*		20
107	575								17 *100*		17
108	580								20 *100*		20

TABLE I—*Continued*

Sample number	Time, hours	Eggs	Larval instars						Pupae	Adults	Total
			1	2	3	4	5	6			
109	585										7
110	590								15 *100*		15
111	595							1 *5.6*	17 *94.4*		18
112	600								17 *100*		17
113	605							2 *10.0*	18 *90.0*		20
114	610								18 *100*		18
115	615							1 *5.9*	16 *94.1*		17
116	620								20 *100*		20
117	625								15 *100*		15
118	630								16 *100*		16
119	635								17 *94.4*	1 *5.6*	18
120	640								19 *100*		19
121	645								18 *100*		18
122	650								19 *100*		19
123	655								17 100		17
124	660								19 *95.0*	1 *5.0*	20
125	665								13 *86.7*	2 *13.3*	15
126	670								12 *66.7*	6 *33.3*	18
127	675								9 *64.3*	5 *35.7*	14
128	680								15 *65.2*	8 *34.8*	23
129	685								7 *46.7*	8 *53.3*	15
130	690								1 *7.1*	13 *92.9*	14

TABLE I—*Continued*

Sample number	Time, hours	Eggs	Larval instars						Pupae	Adults	Total
			1	2	3	4	5	6			
131	695								4 *26.7*	11 *73.3*	15
132	700								2 *11.8*	15 *88.2*	17
133	705								1 *5.6*	17 *94.4*	18
134	710									15 *100*	15
135	720								2 *11.8*	15 *88.2*	17
136	730									17 *100*	17
137	736								1 *5.3*	18 *94.7*	19
138	750								2 *11.2*	16 *88.9*	18
139	760								2 *13.3*	13 *86.7*	15

[1] There was some difficulty with the apparatus here, and samples were mis-timed, and finally Nos. 15 and 16 were spoiled.

[2] This sample should have slipped at 195 hours, but double-contacting of the time-wheel let it go early. Subsequent sample numbers changed to get program on time.

[3] Sampling rate changed to once every three hours until 240 hours.

[4] Sampling rate again changed to once every three hours, hoping to cover the 50% point T.4–5 but it was missed. Such attempts are usually unsuccessful.

[5] Sample spilled and not worth counting.

[6] Data for pupal sexes not shown, as variance so great. More data will be needed for this.

[7] Sample not seeded with eggs, through error.

It is seen from Figure 1 that there is a series of curves, following the rise and fall of each successive life-history stage, with superimposed irregularities due to variable survival from sample to sample. The successive curves cross each other roughly at the 50% line and, if the variance due to mortality be removed, as has been done in Figure 2, they cross *exactly* at this line. We neglect here cases in which more than two life-history stages are present at one time, but will refer to such cases later. These curves are like those obtained by Howe (1950) for the life-history of *Rhizopertha dominica* (F.) but that author could take readings only once per day, thus illustrating the virtues of an autotrephon.

Looking at Figure 2, if we denote the crossing point of the two curves for first and second instar by T.1-2, and the crossing point for those of the second and third instar by T.2-3, then the mean duration of the second instar is the time elapsed from T.1-2 to T.2-3, or $225 - 146 = 79$ hours. (It might be noted here that the value T.1-2 = 146 hrs. is one of the lower values we have obtained for *T. confusum*. A better, mean value is probably about 152 hrs.)

By a continuation of this process, we obtain the values: T.E-1 (115 hr.); T.1-2 (146); T.2-3 (225); T.3-4 (287); T.4-5 (344); T.5-6 (409); T.6-P (528) and T.P-A (683). These yield values for the durations of the successive life history

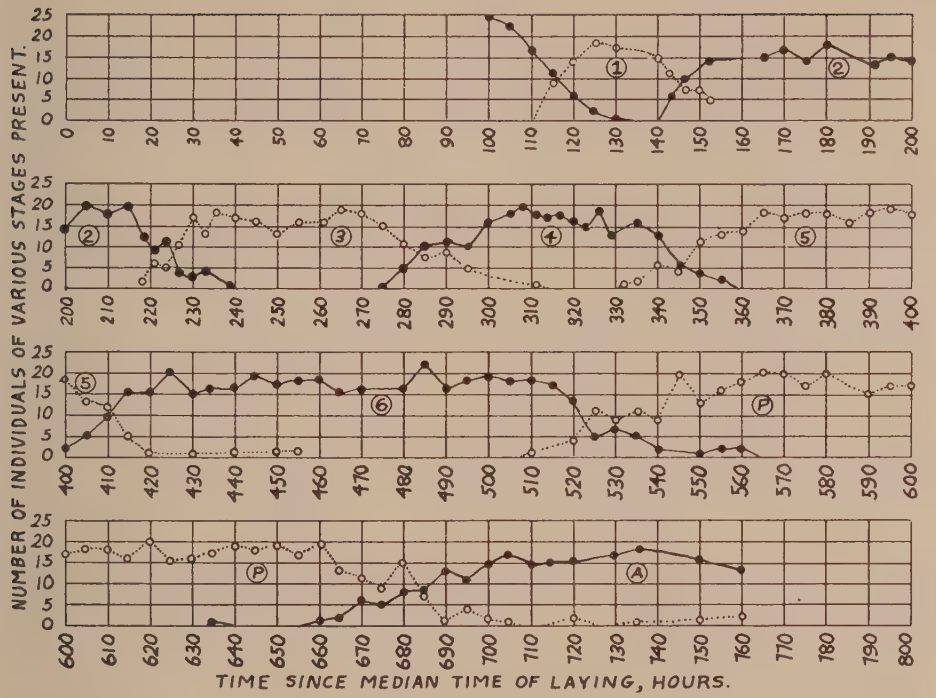

FIG. 1. Numbers of various life-history stages present at time T in a life history of *Tribolium confusum* at 30° C., and 75% R.H. These values are the non-italic values of Table I.

stages of: eggs: 115 hr., first instar: 31 hr., second: 79 hr., third: 62 hr., fourth: 57 hr., fifth: 65 hr., sixth: 119 hr., pupae: 155 hr. However, we are not interested so much in these actual values, as in the method of obtaining them.

The use of the 50%-points is desirable because not only are these points easy to locate, but they are also markedly insensitive to small errors in the smoothing of the curves of Figure 2. It is necessary then to show how Figure 2 is obtained from the data of Table I.

The primary process is that of calculating the percentages of each stage present in a given sample, as percentages of the total survivors, in that sample, thus removing the irregularities due to variations in survival. These percentages are then plotted and smoothed. In doing this, however, difficulty will arise with the egg and first-instar curves. Not only are the individuals very small and inactive, and so likely to be lost in any material which passes the sieves, but also, some of the eggs, though they appear to be viable, and destined to hatch, are like those of the curate in *Punch*, good only in parts. If these duds be counted as good eggs, the point T.1-2 will be misplaced, because the eggs will persist in the samples for many days, until finally, one throws them out as obviously dead.

It is best then, to plot the egg and first-instar curves as well as possible, but to lean heavily on another pair of curves obtained from the egg-timing device of Stanley 1939. In this device, large numbers of eggs of substantially equal age are mounted on a vertical glass plate. This plate is towed at a fixed slow speed over a vaseline-smeared horizontal plate. The larvae fall onto the latter on hatching, and are distributed along it in a time-of-

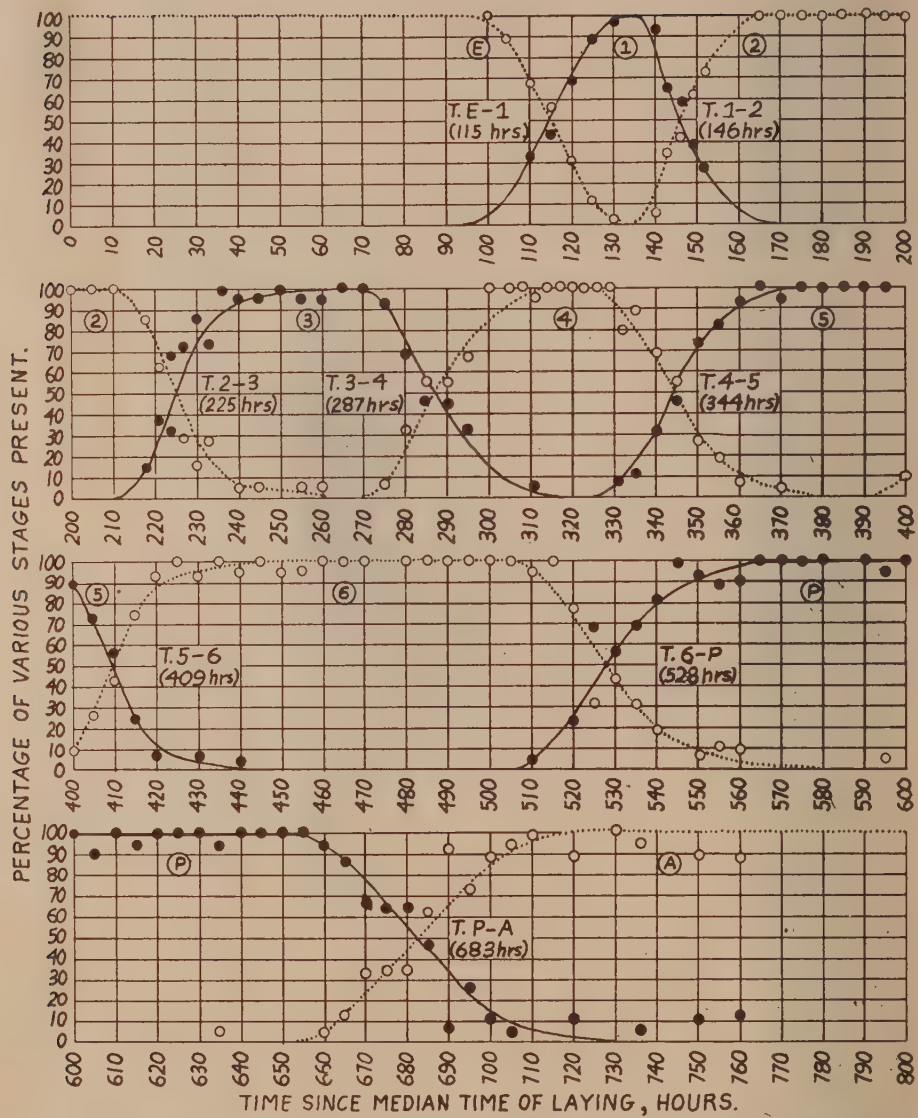
PERCENTAGE OF VARIOUS STAGES PRESENT.
TIME SINCE MEDIAN TIME OF LAYING, HOURS.
T. E-1 (115 hrs.)
T. 1-2 (146 hrs.)
T. 2-3 (225 hrs.)
T. 3-4 (287 hrs.)
T. 4-5 (344 hrs.)
T. 5-6 (409 hrs.)
T. 6-P (528 hrs.)
T. P-A (683 hrs.)

FIG. 2. Percentages of the various life-history stages present at time *T*. These are percentages of the survival at each time, and are the italic values of Table IV up to 152 hrs., and of Table I thereafter.

hatching distribution. Between 500 and 1000 eggs will produce an excellent distribution.

The data from 552 eggs so treated at 30° C., and 75% R.H. are shown in Table II, and plotted as cumulative frequencies in Figure 3. The final survival was 87.8% or 485 eggs. This is not identical with the survival in the autotrephon (64.228%) and some adjustments must be made before the egg-timer curves can be used with the rest of the auto-

trephon data. Normally, the difference will not be as great as this. The large difference in this case facilitates a demonstration of the method of calculation.

We proceed first to plot the values of the last column of Table I, the survivors in each sample, right through the life-history, producing Figure 4. A straight line (or curve if needed) is then fitted to the bulk of the larval data by the method of least squares. To ensure freedom from any "contamination" by uncertain egg and first-instar data, we use data from 191 hrs. onward to 660 hrs., yielding an equation: $S = 16.057 + .003294\ T$, where S is the number surviving and T is time in hours since the median time of laying. The positive coefficient of T would seem to indicate a negative mortality (upward slope of the line) but this of course, cannot be true. What has happened is that there is a small larval mortality (about 3%, according to Stanley, 1946), but so small that it is swamped by the variability between samples. We are forced to assume in this case that there is no larval mortality, and that 16 (16.057) eggs survive out of 25. The others (8.943) die before hatching. This gives a survival of 64.228%. No remarkable accuracy is

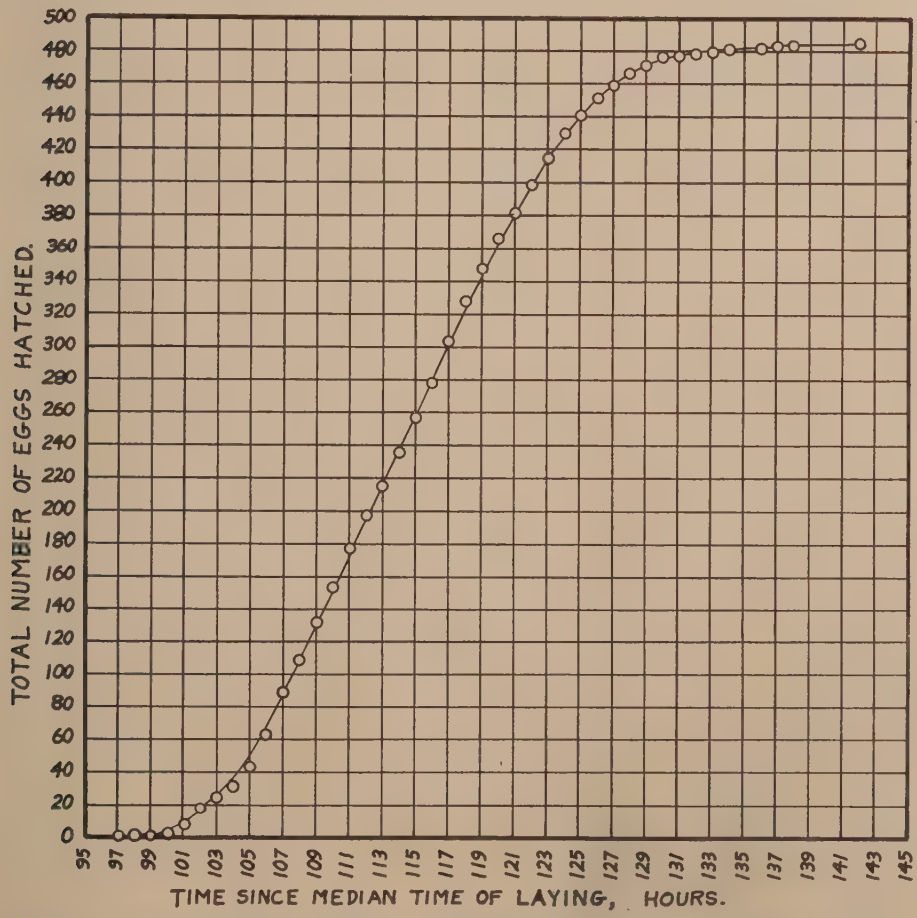

FIG. 3. Cumulative hatching frequencies for 552 eggs, hatched at 30° C., and 75% R.H. on the egg-timing device of Stanley, 1939. These are the values of Table II.

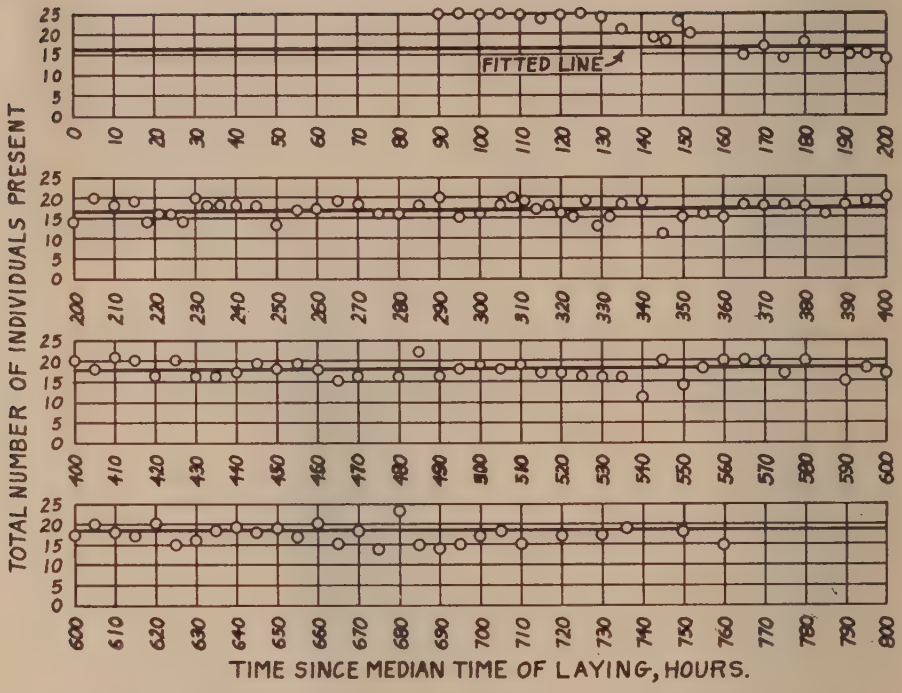

FIG. 4. Total survival of all life-history stages present at time T. These are the values of the last column of Table I, from 191 to 660 hrs. The heavy line is the least squares fit, $S = 16.057 + .0003294\ T$.

implied by the three decimal places. It is necessary to retain three places to preserve the identity of individual values. Rounding off is done at the end of the calculation.

The fitted line fits well in the later regions of the first-instar curve, where there is little trouble with persistent dead eggs, and we may therefore use it as a basis for further calculation.

From the smoothed curve of Figure 3, the values at 5-hr. intervals are picked off as in Column 2 of Table III. Had the egg-timer run shown a survival of 64.228%, a total of 755.5 eggs would have been needed to give 485 survivors. We therefore express the values of Column 2 as percentages of 755.5, as in Column 3. Each value in Column 3 is then determined as a percentage of the final hatch (64.20%) as in Column 4. We can now distribute the 8.943 deaths (out of 25 eggs seeded into the samples) by applying the percentages of Column 4 to 8.943, yielding the values of Column 5. For example, by 120 hrs., $47.91/64.20 \times 100 = 74.63\%$ of $8.943 = 6.67$ eggs are assumed to have died. This process may be open to question, but there does not seem to be any other way to do it, unless one assumes a linear attrition.

Taking the percentages of Column 3 as percentages of 25, we have in Column 6, the numbers of eggs hatched out of 25. It follows that the number *remaining* out of 25 is equal to 25 minus the hatched and minus the dead. At 125 hours this is $25 - 14.59 - 8.13 = 2.28$ $(= 2.3)$, as shown in Column 7.

These adjusted numbers are now combined with the known values for first and second instars from Table I to produce new percentages and totals as in Table IV. We now plot Figure 2, using the percentage values (in italics) from Table

TABLE II. *Frequency distribution in time, of hatching of 552 eggs of* Tribolium confusum *at 30° C., and 75% R.H., yielding a survival of 485 or 87.8%*

Nearest hour of hatching	No. hatching in the hour	Total hatched	Nearest hour of hatching	No. hatching in the hour	Total hatched
96	0	0	120	18	366
97	1	1	121	16	382
98	0	1	122	17	399
99	0	1	123	15	414
100	1	2	124	15	429
101	6	8	125	12	441
102	10	18	126	10	451
103	7	25	127	8	459
104	6	31	128	8	467
105	12	43	129	4	471
106	20	63	130	5	476
107	25	88	131	1	477
108	20	108	132	1	478
109	23	131	133	2	480
110	22	153	134	1	481
111	24	177	135	0	481
112	20	197	136	1	482
113	18	215	137	1	483
114	20	235	138	1	484
115	21	256	139	0	484
116	22	278	140	0	484
117	26	304	141	0	484
118	24	328	142	1	485
119	20	348	143	0	486

IV up to 152 hrs., and those from Table I thereafter. The resultant curves are smoothed by eye, remembering that if there are only two stages present, the curves must cross at the 50% line, and if there are more than two, the sum of the percentages of all forms present must add to 100%. At the same time, the curves must "fit" the data in a smooth reasonable way. It will be found in practice that when this is attempted, there is really only one set of curves which one can reasonably draw. In other words, the above restrictions impose such guidance that one cannot go far wrong, at least, not far enough to move the 50% points any significant amount in time. As a test, the writer has tried smoothing a run at intervals of several successive weeks without looking at previous efforts. There is bound to be some carry-over in this sort of thing, but it was found that one simply could not get much difference in what appeared, by eye, to be the sensible, reasonable set of curves.

If more than two life history stages are present, one must carry out a judicious balancing process between the curves, so that they add to 100%, fit the data, and any two of them cross at 50% if the others are eliminated. This may sound a little like witch-doctory, but again, in practice, it works well. If it does not, one gets more data, until the proper curves are obvious.

It must be borne in mind of course, that there are some basic uncertainties in autotrephon data which cannot readily be removed, that is, there is an uncertainty of ± 0.5 hrs. in the time of laying, and of about ± 0.15 hours due to the time required for cooling in the cool storage.

TABLE III. *Calculation of egg-curve from egg-timer data, with adjustment for the difference in percentage of survival in the egg-timer run and in the autotrephon run*

1	2	3	4	5	6	7
5-hr. intervals	No. of eggs hatching by these times (Fig. 3)	% hatched out of 755.5	% hatched out of final 64.2% hatched	No. dead out of final 8.943 which die	No. hatched out of 25	No. left viable out of 25 (to Col. 3 of Table IV)
95	0	0.00	0.00	0.00	0.00	25.0
100	10	0.13	0.20	0.018	0.03	24.9
105	52	6.88	10.72	0.96	1.72	22.3
110	153	20.25	31.54	2.82	5.23	16.9
115	260	34.41	53.60	4.79	8.60	11.6
120	362	47.91	74.63	6.67	11.98	6.3
125	441	58.37	90.92	8.13	14.59	2.3
130	474	62.73	97.71	8.73	15.68	0.6
135	483	63.90	99.53	8.90	15.97	0.1
140	484	64.06	99.78	8.92	16.01	0.07 (0)
145	485	64.20	100.00	8.94	16.05	0.0

TABLE IV. *Adjusted numbers and percentages of eggs and first and second instar larvae, on basis of egg-hatching data from egg-timer. These values replace those of the first part of Table I*

Sample number	Time, hours	Eggs	Larval instars		Total
			1	2	
1	90	25* *100*			25
2	95	25 *100*			25
3	100	24.9 *100*			24.9
4	105	22.3 *100*			22.3
5	110	16.9 *100*			16.9
6	115	11.6 *56.3*	9 *43.7*		20.6
7	120	6.3 *31.3*	14 *68.7*		20.3
8	125	2.3 *11.2*	18 *88.8*		20.3
9	130	.6 *3.3*	17 *96.7*		17.6
10	140	.1 *.6*	15 *93.2*	1 *6.2*	16.1
11	143†		11 *64.7*	6 *35.3*	17
12	146†		7 *41.2*	10 *58.8*	17
13	149†		7 *38.9*	11 *61.1*	18
14	152†		5 *26.3*	14 *73.7*	19

* From last column of Table III. Decimals rounded off.

† Values at these hours from a smoothed curve through 140, 145, 150, 155 hrs.

For work on the duration of instars, this can mean an uncertainty of ± 1.5 hours in the determination of 50% points. No form of elaborate analysis will remove this. In view of the natural variability of biological material, such an uncertainty is unimportant. No other method known to the writer will produce smaller uncertainties without using an impracticable quantity of data. However, if and when the autotrephon is used for *population* studies, this matter will have to receive further consideration.

It may be added at this point that it has been the writer's experience that, if the technique is rigidly held to a standard, and the environmental controls of the warm chamber are accurate and steady, the results will be so consistent that, if a portion of a life history is missing for any reason, it can be patched-in from a small separate run. This can be done without any discontinuity in the curves being apparent. Probably at this stage, the writer ought to announce that there is a patch in the middle of Figures 1 and 2, and invite the reader to find it (the secret being printed upside down somewhere, to stop people peeking at it). Unfortunately, there is no patch, all the data of the run being a continuous series.[1]

If it seems desirable, a further modification of Figure 2 can be made by plotting it on the basis of mean survival as shown in Figure 5. This can be done by calculation, but can be done more simply by making a sheet of graph paper with the vertical lines as usual, but with the horizontal lines so spaced apart that, at a point where the mean survival is say Y%, 100% on the new scale equals Y% on the basic undistorted scale. In general, this will make the horizontal lines taper together from left to right, and if the general mortality trend is not a straight line, the horizontal lines will be proportionately curved.

One plots Figure 2 on this distorted grid, rubs out the grid, and draws in the usual *undistorted* grid. This will present a picture of the life-history showing the general effect of mortality. In the case

[1] A subsequent paper (Study No. III) will discuss runs done by "reversed tracking" which contain as many "patches" as there are observations, since the observations are not made in chronological order (being sorted into this order at the end of the run). Nevertheless, good curves are obtained.

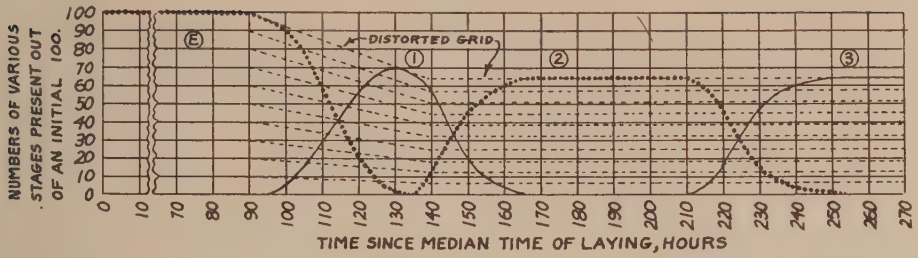

FIG. 5. A portion of the plot of Figure 2, plotted on a distorted grid, to show the effect of average mortality as time passes. The graphs are plotted on the dotted grid, and are read against the solid-line grid.

of our example, with constant, linear mortality in the larvae, the results are not spectacular, but for what it is worth, the first 270 hours of Figure 2 are plotted in this way in Figure 5, with the distorted grid shown by dotted lines.

ACKNOWLEDGMENTS

The writer wishes to express his appreciation of the careful work of Miss Helen J. Martin, who carried out the counts and made up the program for the experiment discussed. He is also indebted to the National Research Council of Canada for financial support of this work.

SUMMARY

In using an autotrephon, a new subbatch is used for the sample of each observation. Therefore the survival does not decline steadily, but oscillates about a mean trend.

A specimen run of the life-history of *Tribolium confusum* Duv., is discussed, the insects being reared at 30° C., 75% R.H., with 25 eggs seeded into samples of 32 gm. of whole wheat flour plus 3% of ground wheat germ. Sampling took place every 5 hours.

The raw data are plotted as percentages of total survival at each observation, removing variability due to variable survival. The egg and first-instar curves are obtained from the egg-timer described by Stanley in 1946, and the data from this are adjusted to account for different mortality in the two pieces of equipment.

Durations of larval instars are determined as the elapsed time between the times at which 50% of one instar has transformed to the next. These points are insensitive to small errors in smoothing the curves.

A final plot can be made whereby the mean survival over the life history is used, plotting on a grid which is vertically distorted to take account of percentage survival at each abscissa. On an undistorted grid, this plots the average survival of each life-history stage throughout the history.

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PRESENT COMPOSITION OF SOME STANDS OF THE FORMER OAK–CHESTNUT FOREST IN THE SOUTHERN BLUE RIDGE MOUNTAINS

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INTRODUCTION

Chestnut blight, caused by the Ascomycete *Endothia parasitica,* was first discovered in the United States in 1904 in New York City and spread rapidly northeast, west, and southwest. By 1910 it had spread as far south as southeastern Pennsylvania and in 1920 the "80 per cent infection zone" extended along the Blue Ridge mountains to central Virginia. In 1926 local infections had been reported in western North Carolina, northern Georgia, and northwestern South Carolina. In 1930 Gravatt and Gill reported that infection in western North Carolina showed eighty to ninety-nine per cent. Owners of chestnut timber in the newly infected areas of the Carolinas and Georgia quickly cut as much of that lumber as possible. Most of the remaining chestnut (*Castanea dentata*)[1] trees, dead or alive, have been gradually removed, until now, twenty years after the blight reached its peak, there are only a few scattered ghost trees left to indicate the once relatively great importance of the species.

The removal of a species which made up more than 40 per cent of the overstory trees in the climax forests of an area would certainly be expected to produce changes in the composition of the vegetation of the region. It is possible that species co-dominant with chestnut would advance in rank and become the most important species in the new climax. It is also possible, as Braun (1950) suggests, that the opening of the canopy, the release of undergrowth trees, and the resulting changes in the humus layer may cause more complex changes than the simple advancement of subordinate species. It would be well to accumulate data from different parts of the original oak-chestnut regions at this time and from time to time in the future so that finally a complete picture of replacement of chestnut can be drawn.

Korstian and Stickel (1927) made studies of this nature in Connecticut, New Jersey, and Pennsylvania to determine the character and amount of natural replacement of blight-killed chestnut. The studies in Connecticut were conducted mainly on permanent plots that were first studied in 1904 before the appearance of chestnut blight. These plots had been mapped and data collected from them at intervals up to 1924. The studies in upper New Jersey and Pennsylvania were on temporary plots from which no records were available before the advent of the blight. Most of the plots studied in all three areas had been selectively cut before or during the period of study. They found that the outstanding feature was the increase of *Quercus rubra* var. *borealis* and *Q. prinus,* both in number of trees and in basal area. They suggested forest management plans for encouraging the better species of oaks. Augesbaugh (1935) reported on the replacement of chestnut in southeastern Pennsylvania 26 years after the first blight was recognized in the area. He treated the blight damages as an exceedingly heavy thinning and found decided growth acceleration among the former associates of chestnut. More than 40 per cent of advance growth and 30 per cent of the reproduction were made up of rock oak (*Quercus prinus*) and red maple (*Acer rubrum*).

[1] Nomenclature of species of vascular plants given without authority is that of Fernald (1950).

The purpose of the present study was to make a record of the replacement of chestnut in an area of the original oak-chestnut association that had not been previously so studied. This record from a southern area of the former oak-chestnut region should prove of value in interpreting the progress being made in the replacement of chestnut in the entire area. To this end, quantitative analyses of the present vegetation were made in a region of the southern Blue Ridge mountains in North Carolina.

Funds for carrying out this investigation were provided by the Margaret Cannon Howell Research Fund of the Highlands Biological Station and a grant from Duke University. Appreciation is due Mr. Henry Wright of Highlands, N. C., for invaluable assistance in field work.

Methods

The stands investigated are all located near Highlands in Macon County, North Carolina. This is near the southern limit of the former oak-chestnut association which extended in a northeast-southwest direction from New England and the Hudson River valley to northern Georgia (Braun 1950).

There are no reliable records of the preblight compositions of the forests of the region. However, people who were living there at that time estimated that as much as 40 per cent of the large trees were chestnuts, and that the chestnuts were more abundant on the sides of the mountains than in the coves and on the rocky mountain-tops. A large part of the area has been part of the Nantahala National Forest since before the advent of the chestnut blight. Most of the chestnut trees were cut from the National Forest lands soon after the blight became widespread in the area, and the only stands that have been left undisturbed except for chestnut blight are privately owned. Although these privately owned stands are usually smaller than those located in the National Forest, they were chosen for study because of their undisturbed condition. Consideration of exposure in choosing the stands to be studied was necessary because almost all sites in the area have considerable slope and because there are some obvious differences in the vegetation of slopes of different exposures. The criteria for choosing stands to be studied were: first, that they be undisturbed by fire, cutting, cultivation, or other agents except chestnut blight; second, that they be located on the sides of the mountains, where chestnuts were formerly abundant; and third, that half of them have northern exposures and half, southern exposures. Six stands meeting these requirements were found near Highlands.

Stand I was located on a southeastern exposure about 6 miles south of Highlands near Ammons Camp Ground. This stand had the lowest elevation of the 6 stands studied, lying between 2,800 and 2,900 feet above sea level. Stand II was located on a southwest slope about 3 miles northwest of Highlands and a few hundred yards south of U. S. Highway 64 at an elevation of 3,800 to 4,000 feet. Stand III was on a southwest slope above Bridal Veil Falls about 3 miles northwest of Highlands on U. S. Highway 64, at an elevation of 3,400 to 3,600 feet. Stand IV was on a gentle north-facing slope with an elevation of about 4,200 feet and was located about 6 miles north of Highlands on the Buck Creek road. Stand V was on a north-facing slop located within the city limits of Highlands between Trillium Lodge and Satulah Mountain at an elevation of 4,000 to 4,200 feet. Stand VI was on a north-facing slope between 3,800 and 4,000 feet about 5 miles northeast of Highlands near U. S. Highway 64 in the vicinity of Whitesides Mountain. Degree of slope was not determined because of the slope variations within each stand.

Composition of the vegetation in each stand was determined by use of ten quadrats in each of 3 sizes. In 10×10 meter quadrats, list-counts were made and diameters taken of all woody species

over 10 feet in height or over one inch d.b.h. (diameter breast high). The hickories (*Carya*) were counted as a group and no effort was made to distinguish species. In most cases it would have been possible to distinguish the species of the larger hickories, but young plants are extremely difficult to identify to species. Overstory and understory trees were recorded separately. Many trees recorded and measured as overstory trees were much smaller than the dead or dying chestnuts that once occupied the areas, but at the present time they are the tallest individuals present. Chestnut trees that showed some living branches were counted and measured in the size class to which they belonged. Woody plants less than 10 feet high or 1 inch d.b.h. were listed in ten 4×4 meter quadrats. These were separated into two sizes, the transgressive class from 1 foot to 10 feet high and the seedlings less than 1 foot high. Herbaceous plants were listed in ten 2×2 meter quadrats. The three sets of quadrats were "nested" and distributed in each stand at 20 meter intervals along lines running parallel to the slope. In most of the stands two, but sometimes three, such lines were used.

Density and frequency of each species by size classes were calculated from the data obtained from the quadrats. Basal areas for the overstory trees and percentages of total basal area for each species were calculated.

Results

A. Overstory trees

Fifteen kinds of trees were found in the overstory layer of the 6 stands (Table I). Eight of these species were represented on both north-facing and south-facing slopes: northern red oak (*Quercus rubra* var. *borealis*) chestnut-oak (*Quercus prinus*), hickory (*Carya ovalis* and/or *C. glabra*), white oak (*Quercus alba*), chestnut, red maple (*Acer rubrum*), sourwood (*Oxydendrum arboreum*) and scarlet oak (*Quercus coccinea*). Four species were found as overstory trees on south-facing slopes only: yellow poplar (*Liriodendron tulipifera*), white pine (*Pinus strobus*) silverbell (*Halesia carolina*) and sassafras (*Sassafras albidum*). Three species were found in the quadrats

Table I. *Percentage of basal area (% B.A.),[1] density (D),[2] and frequency (F)[3] of overstory trees in sixty 10 × 10 m. quadrats in the Highlands region*

Species	Total			North-facing slopes			South-facing slopes		
	% B.A.	D	F	% B.A.	D	F	% B.A.	D	F
Quercus rubra var. *borealis*	24.44	.43	35	16.62	.47	43	31.79	.40	27
Quercus prinus	22.21	.50	37	32.97	.63	43	13.53	.37	30
Carya glabra and *C. ovalis*	16.63	.43	30	4.59	.13	10	26.42	.83	50
Quercus alba	9.23	.15	12	3.46	.03	3	13.93	.27	20
Castanea dentata	8.84	.17	13	17.51	.27	20	1.75	.07	7
Acer rubrum	2.52	.13	10	4.02	.20	17	1.31	.07	3
Oxydendrum arboreum	1.30	.05	5	1.95	.03	3	0.78	.07	7
Quercus coccinea	1.23	.03	3	0.83	.03	3	1.51	.03	3
Betula lenta	5.67	.12	12	12.65	.23	23			
Robinia pseudo-acacia	1.30	.07	7	2.91	.13	13			
Nyssa sylvatica	1.08	.02	2	2.43	.03	3			
Liriodendron tulipifera	4.90	.03	3				8.89	.07	7
Pinus strobus	0.43	.08	3				0.79	.17	7
Halesia carolina	0.14	.02	2				0.13	.03	3
Sassafras albidum	0.02	.02	2				0.03	.03	3

[1] Percentage of basal area, being based on both size and number of individuals, gives the best indication of dominance in a plant community.

[2] Density is used to indicate the number of individuals per quadrat in the stands and is no indication of how these individuals are distributed in the stands.

[3] Frequency denotes the number of quadrats in which a species occurs as expressed in per cent of total quadrats used. Frequency is thus an expression of the uniformity of distribution of a species.

on the north-facing slopes only: cherry birch (*Betula lenta*), black locust (*Robinia pseudo-acacia*) and black gum (*Nyssa sylvatica*). Northern red oak, chestnut oak, white oak, hickory and chestnut made up 81.35 per cent of the total basal area and 75 per cent of the individuals counted. According to percentage of total basal area of overstory trees for the entire area, northern red oak ranked first in importance, chestnut oak second, hickory third, white oak fourth, and chestnut fifth.

1. South-facing slopes.—Although the five major components were present on both exposures, there were noticeable differences in the relative importance of these species on the north-facing and south-facing slopes. Judging by the percentage of basal area of overstory trees on the south-facing slopes, northern red oak was the most important tree. The second in importance was hickory, followed in turn by white oak, chestnut oak, and chestnut. Overstory chestnut trees showing any sign of life appeared only occasionally on the south-facing slopes and only two such specimens fell within the quadrats. Most of the dead chestnut trees had fallen to the ground and were in advanced stages of decay. No white oak appeared in the overstory records of Stand I in which hickories were most abundant, and where northern red oak and chestnut oak were present in lesser numbers. In Stand II, where white oaks

TABLE II. *Density (D) and frequency (F) of understory trees in sixty 10 × 10 m. quadrats in the Highlands region*

Species	Total		North-facing slopes		South-facing slopes	
	D	F	D	F	D	F
Potential overstory trees						
Quercus rubra var. *borealis*	2.02	57	2.90	53	1.13	60
Acer rubrum	1.97	63	0.90	50	3.03	77
Carya glabra and *C. ovalis*	1.77	52	0.53	30	3.00	73
Castanea dentata	1.57	70	2.00	83	1.13	57
Quercus prinus	1.03	50	0.83	45	1.23	50
Quercus alba	0.50	28	0.43	17	0.57	40
Halesia carolina	0.48	23	0.60	23	0.37	23
Liriodendron tulipifera	0.40	10	0.27	10	0.53	10
Pinus strobus	0.27	15	0.07	7	0.47	23
Sassafras albidum	0.27	13	0.43	20	0.10	3
Nyssa sylvatica	0.27	18	0.30	23	0.23	13
Betula lenta	0.25	15	0.47	27	0.03	3
Tsuga canadensis	0.20	17	0.13	13	0.27	20
Robinia pseudo-acacia	0.17	13	0.23	17	0.10	10
Oxydendrum arboreum	0.17	13	0.03	3	0.30	23
Prunus serotina	0.17	10	0.33	20		
Betula lutea	0.03	3	0.07	7		
Magnolia acuminata	0.02	2	0.03	3		
Quercus coccinea	0.13	13			0.27	27
Quercus velutina	0.05	5			0.10	10
Fraxinus americana	0.02	2			0.03	3
Secondary trees and shrubs						
Cornus florida	3.13	48	0.03	3	6.23	93
Rhododendron calendulacea	0.75	23	1.07	30	0.43	17
Rhododendron maximum	0.42	23	0.20	17	0.63	30
Hammamelis virginiana	0.42	17	0.47	17	0.37	17
Acer pensylvanicum	0.08	8	0.13	13	0.03	3
Kalmia latifolia	0.08	8	0.07	7	0.10	10
Castanea pumila	0.03	3			0.07	7
Vaccinium corymbosum and V. vacillans Kalm.	0.23	12	0.47	23		
Clethra acuminata	0.22	7	0.43	13		
Amelanchier spp.	0.05	3	0.10	7		
Ilex monticola	0.05	5	0.10	10		

were most abundant, hickories did not appear in the overstory records.

2. North-facing slopes.—Chestnut oak was the most important tree on north-facing slopes. It was followed in turn by chestnut, northern red oak, and white oak. Living chestnuts were still abundant on north-facing slopes. All of the chestnut individuals large enough to be counted in the overstory were badly diseased and usually possessed only a few living branches. Consequently the influence they exerted in the community was not nearly as great as their basal area would indicate. Perhaps the chestnut trees on the north-facing slopes were attacked later by the fungus, or else the diseased trees were able to live there longer than on the south-facing slopes. The abundance of white oak and hickory was much less on north-facing slopes than on slopes with southern exposure.

B. Understory plants

Table II gives the density and frequency of all plants found in the understory in sixty 10 × 10 m. quadrats in the stands studied. This table is made up of

TABLE III. *Density (D) and frequency (F) of woody plants from one to ten feet tall (transgressives and shrubs) found in sixty 4 × 4 m. quadrats in the Highlands region*

Species	Total		North-facing slopes		South-facing slopes	
	D	F	D	F	D	F
Potential overstory trees						
Castanea dentata	1.60	65	1.47	57	1.73	73
Quercus prinus	1.22	32	1.83	23	0.60	40
Acer rubrum	0.58	40	0.33	27	0.83	53
Cara ovalis and *C. glabra*	0.57	28	0.17	13	0.97	44
Sassafras albidum	0.52	23	0.37	20	0.67	27
Quercus rubra var. *borealis*	0.48	30	0.40	30	0.57	30
Nyssa sylvatica	0.22	12	0.07	7	0.37	17
Liriodendron tulipifera	0.15	13	0.03	3	0.27	23
Robinia pseudo-acacia	0.10	10	0.10	10	0.10	10
Quercus alba	0.10	8	0.03	3	0.17	13
Tsuga canadensis	0.05	5	0.03	3	0.07	7
Prunus serotina	0.03	3	0.07	7		
Magnolia acuminata	0.03	3	0.07	7		
Betula lenta	0.02	2	0.03	3		
Halesia carolina	0.28	18			0.57	37
Quercus coccinea	0.13	7			0.27	13
Fraxinus americana	0.05	3			0.10	7
Quercus velutina	0.03	2			0.07	3
Oxydendrum arboreum	0.03	3			0.07	7
Pinus strobus	0.02	2			0.03	3
Secondary trees and shrubs						
Gaylussacia ursina (M. A. Curtis) T. and G.	17.00	60	26.57	73	7.43	47
Rhododendron calendulacea	0.73	22	1.03	23	0.43	20
Vaccinium corymbosum and *V. vacillans* Kalm.	0.48	10	0.30	13	0.67	7
Kalmia latifolia	0.12	12	0.10	10	0.13	13
Amelanchier spp.	0.07	7	0.07	7	0.07	7
Rhododendron maximum	0.05	5	0.03	3	0.07	7
Leucothoe editorum	0.60	15	1.20	30		
Menziesia pilosa	0.27	5	0.53	10		
Clethra acuminata	0.10	5	0.20	10		
Rhododendron arborescens	0.08	3	0.17	7		
Ilex monticola	0.07	5	0.13	10		
Magnolia fraseri	0.05	3	0.10	7		
Rhododendron catawbiense	0.03	3	0.07	7		
Symplocos tinctoria	0.03	3	0.07	7		
Cornus florida	0.65	30			1.30	60
Hamamelis virginiana	0.03	3			0.07	7

32 kinds of plants, 21 of which have genetic possibilities of becoming overstory trees, and 11 of which do not. Nine of these kinds of plants make up 76.9 per cent of the entire understory population. Included in this number are six potential overstory trees: northern red oak, red maple, hickory, chestnut oak, and white oak; and three other species: dogwood (*Cornus florida*), great Rhododendron (*Rhododendron maximum*) and flame azalea (*Rhododendron calendulacea*) which are shrubs or small trees.

In this layer considerably more red maple and hickory were found on the southern exposures than on the northern ones, and somewhat more northern red oak and chestnut on the north-facing slopes than on the south-facing ones. Dogwood was the most abundant species in the understory layer on the southern exposure, making up 30 per cent of the total number of individuals present. However, dogwood was almost entirely absent from the north-facing slopes with only one specimen in any size class being found on that exposure. Flame azalea was recorded from two south-facing stands and from two north-facing ones with considerably higher density on the northern exposure. Great Rhododendron was present in all of the south-facing stands and in lesser densities in two of the north-facing stands. This species does not make the dense stands on the middle slopes that it does under hemlocks in coves but is consistently present in scattered clumps.

C. Transgressives

Thirty-six kinds of plants were represented in the quadrat counts for the entire area in the transgressive layer, 28 on the north-facing slopes and 25 on the south-facing slopes (Table III). Buckberry (*Gaylussaccia ursina* (M. A. Curtis) T. and G.) was the most abundant species in the layer, far outnumbering all the other plants together. Forty-three per cent of the individuals on the south-facing slopes and 73 per cent of those on the north-facing slopes belonged to this species. An average of 27 buckberry plants was found per 4 × 4 meter quadrats on the northern exposures. This was sufficient to form almost impenetrable masses of shrubs 3 or 4 feet high. Ten other kinds of plants were abundant enough to be of importance in this layer. The following 10 species and the buckberries made up 93.4 per cent of the total population of the transgressive and shrubby layer: chestnut, chestnut oak, red maple, hickory, sassafras, northern red oak, flame azalea, dog hobble (*Leucothoe editorum*), blueberries (*Vaccinum corymbosum* and *V. vacillans* Kalm) and dogwood. Chestnut, hickory, and northern red oak were present in all six stands; chestnut oak was found in this layer in two north-facing stands and two south-facing stands; white oak was counted in two south-facing stands and in only one north-facing stand in this layer. Besides buckberry, flame azalea and dog hobble were considerably more numerous on the northern exposures than on the southern; red maple was more abundant on south-facing slopes than on north-facing ones. Dogwood was completely absent in this layer on northern exposures.

D. Woody seedlings

A total of 27 kinds of woody seedlings (Table IV) were found in the sixty 4 × 4 meter quadrats counted, 18 species on the northern exposures and 22 on the southern. The following 10 species made up 96.7 per cent of the total woody seedlings found: white oak, chestnut oak, red maple, northern red oak, hickory, chestnut, sassafras, buckberry, dogwood, and blueberries. This list of the most important woody seedlings contains all five of the major components of the upperstory of the region. Chestnut and red maple were recorded in all six stands; chestnut oak and northern red oak in five; sassafras and hickory in four; and white oak in only three. In Stand III, where there were a number of large white oaks in the

TABLE IV. *Density (D) and frequency (F) of woody plants less than 1 foot high (seedlings) in sixty 4 × 4 m. quadrats in the Highlands region*

Species	Total		North-facing slopes		South-facing slopes	
	D	F	D	F	D	F
Potential overstory trees						
Quercus alba	5.85	23	0.33	3	11.37	43
Quercus prinus	3.88	33	0.43	17	7.33	50
Quercus rubra var. *borealis*	1.48	52	1.63	57	1.33	47
Carya glabra and *C. ovalis*	1.33	37	0.07	7	2.60	67
Acer rubrum	1.05	52	0.83	40	1.27	63
Castanea dentata	0.43	30	0.30	27	0.57	33
Sassafras albidum	0.38	13	0.23	3	0.53	23
Halesia carolina	0.22	12	0.03	3	0.40	20
Liriodendron tulipifera	0.22	17	0.03	30	0.40	3
Magnolia acuminata	0.02	2	0.03	3		
Nyssa sylvatica	0.17	8			0.33	17
Fraxinus americana	0.05	2			0.10	3
Quercus coccinea	0.05	3			0.10	7
Oxydendrum arboreum	0.05	5			0.10	10
Quercus velutina	0.05	3			0.10	7
Pinus strobus	0.03	3			0.07	7
Secondary trees and shrubs						
Gaylussaccia ursina (M. A. Curtis) T. and G.	22.05	50	39.17	73	4.93	27
Vaccinium corymbosum and V. vacillans Kalm.	0.38	12	0.17	13	0.60	10
Amelanchier spp.	0.12	10	0.20	13	0.03	7
Magnolia fraseri	0.05	5	0.07	7	0.03	3
Leucothoe editorum	0.15	2	0.30	3		
Acer pensylvanicum	0.03	2	0.07	3		
Ilex monticola	0.03	3	0.07	7		
Rhododendron calendulacea	0.02	2	0.03	3		
Cornus florida	0.66	27			1.33	53
Hamamelis virginiana	0.05	2			0.10	3
Kalmia latifolia	0.03	2			0.07	3

overstory, the number of white oak seedlings was exceedingly high, averaging 33 per 4 × 4 meter quadrat: In the other two stands where it appeared, the densities were only 1.1 per quadrat. Buckberry was abundant in this layer, as in the transgressive and with much higher density on the northern exposures than on the southern.

E. Herbaceous vegetation

An established climax community has its characteristic herbs and the opening of the forest canopy usually has noticeable effects on the lower layers of plants. There may have been and probably will continue to be changes for some time in the herbaceous plants in the former oak-chestnut forests. This report cannot show what changes have been made in the herbaceous plants of the area since the removal of chestnuts by blight but it can help to give a complete picture of the communities as they now exist.

Fifty kinds of herbs, usually recorded as species, but sometimes as genera, were represented in sixty 2 × 2 meter quadrats counted in the six stands (Table V). Thirty-three were found on south-facing slopes and 38 on the northern exposures. Thirteen species, each of which represented at least one per cent and together made up 72.6 per cent of the total herb population, are included in the following list: *Dryopteris noveboracensis, Galax aphylla, Smilacina racemosa, Potentilla simplex, Chimaphila maculata, Eupatorium rugosum, Dennstaedtia punctilobula, Lysimachia quadrifolia, Uvularia sessifolia, Osmunda cinnamomea, Trillium catesbaei* Ell., *Prenanthes trifoliata,* and *Veratrum viride.* Several genera

showed higher densities than some species included in the list above, but since it was not possible to determine species within these genera, the importance of such species could not be evaluated. *Drypoteris noveboracensis* was the most characteristic species in the area, being present in all stands with high density and frequency on both exposures. *Smilacina racemosa, Chimaphila maculata* and *Lysimachia quadrifolia* were in all six stands but with considerably higher densities on the southern exposures. *Eupatorium rugosum,* present in all six stands, had twice

TABLE V. *Density (D) and frequency (F) of herbaceous plants found in sixty 2 × 2 m. quadrats in the Highlands region*

Species	Total		North-facing slopes		South-facing slopes	
	D	F	D	F	D	F
Dryopteris noveboracensis	13.43	75	14.33	77	12.53	73
Galax aphylla	5.20	8	6.57	7	3.83	10
Smilacina racemosa	3.00	43	1.57	43	4.43	43
Chimaphila maculata	2.27	40	0.90	13	3.63	67
Viola spp.	1.98	55	1.10	37	2.87	73
Desmodium spp.	1.66	28	0.20	37	3.13	20
Eupatorium rugosum	1.35	38	1.93	33	0.77	43
Lysimachia quadrifolia	1.12	33	0.83	37	1.40	30
Dioscorea spp.	0.98	28	0.77	33	1.20	23
Solidago spp.	0.80	40	1.10	53	0.50	27
Uvalaria sessilifolia	0.80	27	0.83	30	0.77	23
Trillium catesbaei Ell.	0.66	37	0.40	33	0.93	40
Smilax spp.	0.63	37	0.20	13	1.07	60
Rubus spp.	0.45	25	0.53	23	0.37	27
Mediola virginiana	0.37	18	0.63	23	0.10	13
Streptopus amplexifolius and *S. roseus*	0.33	10	0.23	17	0.43	3
Clintonia umbellulata	0.28	7	0.47	10	0.10	3
Euphorbia corollata	0.17	13	0.13	17	0.20	10
Melampyrum lineare	0.12	5	0.17	3	0.07	7
Gillenia trifoliata	0.12	8	0.20	13	0.03	3
Gerardia tenuifolia	0.05	3	0.07	3	0.03	3
Dennstaedtia punctilobula	1.33	17	2.67	33		
Osmunda cinnamomea	0.75	17	1.50	33		
Prenanthes trifoliata	0.57	17	1.13	33		
Veratrum viride	0.48	13	0.97	27		
Arisaema atrorubens	0.35	10	0.70	20		
Polygonatum biflorum	0.27	8	0.53	17		
Thalictrum clavatum	0.25	7	0.50	13		
Aralia racemosa	0.15	10	0.30	20		
Stenanthium gramineum	0.12	7	0.23	13		
Pedicularis canadensis	0.12	5	0.23	10		
Athyrium felix-femina var. *asplenoides*	0.12	2	0.23	3		
Houstonia purpurea	0.05	5	0.10	10		
Actaea alba (L.) Mill.	0.03	2	0.07	3		
Pteridium aquilinum var. *latiusculum*	0.03	3	0.07	7		
Aruncus dioicus	0.02	2	0.03	3		
Collinsonia canadensis	0.02	2	0.03	3		
Ligusticum canadense	0.02	2	0.03	3		
Potentilla simplex	2.53	35			5.07	70
Parthenocissus quinquefolia	0.62	3			1.23	7
Goodyera pubescens	0.32	7			0.63	13
Panicum sp.	0.17	3			0.33	7
Monarda clinopodia	0.15	5			0.30	10
Galium spp.	0.12	5			0.23	10
Polystichum acrostichoides	0.12	10			0.23	20
Dryopteris hexagonoptera	0.10	2			0.20	3
Cypripedium acaule	0.05	5			0.10	10
Corallorhiza odontorhiza	0.03	2			0.07	3
Gaultheria procumbens	0.02	2			0.03	3
Cypripedium calceolus var. *pubescens*	0.02	2			0.03	3

as great a density on north-facing slopes as on south-facing ones. *Trillium catesbaei,* present in all six stands, and *Uvularia sessilifolia,* present in all but one north-facing stand, showed little difference in abundance on either exposure. *Dennstaedtia punctilobula, Osmunda cinnamomea* and *Prenanthes trifoliata* were present in high densities on the north-facing slopes but were not recorded on the south-facing slopes. *Potentilla simplex* was found only on the southern exposures. *Galaz aphylla* is not as important on the middle slopes of the region as the high density would indicate; it was recorded in only one of the north-facing slopes and one of the south-facing ones. In those quadrats where it did appear, it usually made an almost complete ground cover.

Correlations

When the extent of the damage being caused by chestnut blight first became apparent, many people hoped that seeds from diseased trees might produce a strain of resistant chestnuts. However, reports from northern areas show these hopes to be groundless. The Connecticut Agricultural Experiment Station (1931) reported that by 1931 mature nuts from chestnut sprouts arising from diseased trees were common in Connecticut and that although seedlings from such nuts might become fifteen or twenty feet tall before gradually contracting the disease, they all finally died. It also reported that sprouts from stumps succumbed more quickly than seedlings.

The removal by blight of chestnut from the forests in the southern Blue Ridge Mountains has been a gradual process covering some twenty years and has not yet become complete. There is little evidence that the species will survive in the southern parts of its range any more than it did in the north. The infection was later in arriving in the southern areas. This fact apparently accounts for the number of chestnuts still living there. All chestnut individuals present before 1927 are badly diseased and without doubt will finally die. Even the fact that diseased trees are still producing seeds and that there is an abundance of smaller-sized chestnut plants, undoubtedly offspring of the diseased trees, raises little hope for the final survival of the species in these areas.

Practically all of the younger chestnuts reported in this study were seedlings and not sprouts. It was originally intended to separate seedlings from sprouts in the data, but this seemed impossible in the counts on the south-facing slopes which were made first. It was not until the field work was being done on the north-facing slopes later and a few unmistakable sprouts were found, that it was realized that the supposed difficulty in distinguishing sprouts from seedlings arose from the fact that there were very few sprouts on south-facing slopes. Most of the original chestnuts on the southern exposures have probably been dead so long that the sprouts which arose from such trees have long since come and gone. It is certainly an unfounded hope, in spite of the still living older chestnut trees and the large number of younger plants, that the species will survive in the south.

The present plant communities in the Highlands region are certainly successional ones because twenty years is too short a time for a new equilibrium to be established after the major disturbance caused by the decrease in number of the chestnuts. It is not known what changes in rank of importance of species has taken place during the time in which the chestnuts have been dying or what will be the composition of the forests when equilibrium is finally established. However there may be enough evidence at this time to speculate on what species will be present when equilibrium is established.

A large number of seedlings does not always indicate the future importance of a species in a given community because conditions may be suitable for germination but not for continued growth. However, if a species is present in all size

classes and these individuals are well distributed throughout the community, that condition indicates that the species may continue to hold its place in the community. Although there is no hope of chestnut remaining as a part of the eventual climax in the southern Blue Ridge Mountains, there is enough reproduction in all size classes of northern red oak, chestnut oak, hickory, and white oak to predict their presence but not necessarily their order of importance in the future plant communities of the area.

Northern red oak now ranks first in the overstory and first of the potential overstory trees in the understory. It drops to sixth place in the transgressive layer and is third in the seedlings. This amount of reproduction in all layers indicates that this species will continue to be among the most important ones in the area but may not continue to hold its first ranking position. Chestnut oak will certainly be present in substantial numbers in the future forests of the region. It now ranks fifth in the understory, second in the transgressive layer and second among the seedlings. The hickories hold second rank on the southern exposures in every layer at the present time and although not so important on the northern exposure it should remain important in the area. White oak is generally more abundant on southern exposures than on northern ones but at times is completely absent in stands on either exposure. A very great number of white oak seedlings in one south-facing stand makes this species seem much more important in that layer than it really is. White oak should be present in the future forests, but probably will exhibit a scattered distribution as it does at present.

Red maple is present in considerable numbers in the three lower layers of the forests of the region, but the possibility of its becoming one of the major overstory trees is not great. Oosting (1942) reports this species abundantly present in the lower forest layers in the Piedmont of North Carolina but not in the overstory, and the same could probably be true of this species in the Highland region.

It is customary to call a forest region by some combination of the most important trees in the overstory. If northern red oak, chestnut oak, hickory and white oak continue to be the most abundant overstory trees in the forests of the southern Blue Ridge mountains, it should be called "oak-hickory." Oosting (1942) calls the climax vegetation of Piedmont North Carolina oak-hickory. Braun (1950) calls the climax vegetation of certain regions in the central and south-central part of the United States oak-hickory. All of these—the Highlands area, the Piedmont of North Carolina, and the oak-hickory regions in the central part of the United States—have certain things in common. The most important trees belong to some species of oaks, and some species of hickory are always present although in smaller numbers than the oaks. Some species of oaks are present in all three places in varying degrees of importance and some species of oaks that are highly important in one of three places are entirely absent from one or both of the others. A number of the same or closely related smaller associates are present in all three regions but vary in importance from one region to another. Although the plant communities now present on the slopes of the Highlands region are not climax because a state of equilibrium has not been reached following the gradual decrease of chestnuts, the reproduction of potential overstory trees indicates that the major trees will continue to be species of oaks and hickories. By the accepted custom of naming the forests of a region by the most important overstory trees it will not be inconsistent to call those of the Highlands region oak-hickory.

Conclusions and Summary

Although there are still many chestnut trees, especially in the smaller size-classes in the Highlands section of the southern Blue Ridge Mountains, there is little hope that the species will survive

there any more than it did in the northern parts of its range. Since the chestnut is almost gone and will certainly never again be among the dominant trees in the climax forests of the region, the association is no longer oak-chestnut and should not continue to be called by that name.

It has been too short a time since the chestnuts began to die for an equilibrium to be established, but there is some evidence at this time as to what the new climax may be. At the present time, the dominant species in the communities on the middle slopes, where the former oak-chestnut climax existed, consist mainly of oaks and hickories with northern red oak, chestnut oak, and white oak being the most abundant oaks. Reproduction in all size classes indicates that these species should maintain their place among the dominants of the future climax. Data should be collected from the former oak-chestnut regions now and at intervals in the future to see whether this trend is continued or not. If it is found that the oaks and hickories now present in the former oak-chestnut stands do continue to maintain their dominance, the forests of the region could best be considered as a part of the more widespread oak-hickory forests.

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HIBERNATION STUDIES OF TWO SPECIES OF SALAMANDERS, *PLETHODON CINEREUS CINEREUS* AND *EURYCEA BISLINEATA BISLINEATA*

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Hibernation is a subject of extremely broad biological interest, and many different lines of study have been explored by workers in this field. The present paper deals with the hibernation of two species of salamanders, *Plethodon cinereus cinereus* (Green), the red-backed salamander, and *Eurycea bislineata bislineata* (Green), the two-lined salamander. Field studies were made, the reactions of these two species to a soil temperature gradient were studied in the laboratory, and seasonal changes in the body water content of *P. cinereus* were investigated.

I am grateful to C. J. Goodnight, under whose direction this study was made, and am indebted to C. F. Shutts, from whom climatic data of Ross Biological Reserve were obtained, and to R. E. Tashian for valuable field assistance. This work was made possible by a grant from the Purdue Research Foundation.

Some observations on the hibernation of these salamanders are found in the literature (Blanchard 1928, 1933; Grizzell 1949; McClure 1943; and Neill 1948).

Most experimental studies on the response of amphibians to a thermal change have been restricted to frogs (Bohnsack 1951). Rogers and Lewis (1916) have made laboratory studies in which salamanders were used.

The vital limits of water loss in some plethodontid salamanders, including *Plethodon cinereus,* were studied by Littleford *et al.* (1947). Stebbins (1945) stated that salamanders increased their body weight by water absorption after the first fall rains and thus appeared well-nourished. Although it is apparent that in certain groups of animals, especially some insects, a decrease in body water precedes winter, seasonal change of the percentage of body weight composed of water in salamanders has not been extensively studied.

Materials and Methods

Hibernation of *Plethodon cinereus* and *Eurycea bislineata* was observed on two enclosed plots of soil, measuring 36 × 36 × 36 inches. These enclosures were constructed by removing the soil in such a fashion that an island remained. A wire screen with a one-eighth inch mesh was placed around the square island, the free ends of the screen were united, and then the soil was replaced. The wire extended about eight inches above the level of the ground. After the animals were introduced into these cages a wire screen lid was placed over the top, eliminating the possibility of escape by the animals.

The site of these cages was in the Ross Biological Reserve, which is owned by Purdue University. Ross Biological Reserve is an area mostly covered with mixed mesophytic forest. The location of the cages was in a ravine approximately ten feet from a stream where the soil type is Eel Sandy Loam (according to an unpublished M.S. thesis by C. R. Faulkner at Purdue University). Both species of salamanders are found naturally in the immediate vicinity of these sites.

In this study the enclosures were prepared during July, 1950, but the animals were not placed in the cages until November, 1950. This was done to permit the habitat to recover from any disturbance caused by the earlier digging On November 1, 1950, a total of 51 specimens of *Plethodon cinereus* and six of *Eurycea bislineata* were placed in the two cages

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and the lids were firmly fixed in position. In addition to the normal leaf mold in the cages, decaying logs were placed in each enclosure. One of the enclosures was opened February 22, 1951, the other on February 27; by very careful inspection of the soil within the limits of the wire screen, the specimens present were recovered.

Air temperature, soil temperature, and soil moisture content were recorded. The last two readings were taken at the exact recovery site of each animal. The percentage of soil moisture was determined by the standard wet-weight dry-weight technique. All results are in per cent of water based on total wet weight. The depth of burrowing, position of the animal, description of the hibernaculum, and general observations were also noted for each recovered specimen.

As an indication of the general climatic picture during the period of this experiment, records of the air temperature and soil temperature at depths of three inches, nine inches, and eighteen inches were obtained. A Foxboro recording thermograph recorded soil temperature and a Tempscribe registered the air temperature.

Reactions of these two species of salamanders to a soil temperature gradient was studied by the following technique. A temperature gradient was established by placing a lamp with a red-light bulb a known distance beneath a 2,000 ml beaker filled with a loose silty loam type of soil. A sheet of asbestos insulating material was placed around the beaker and extended continuously downward over the bulb of the lamp. In this manner, the insulating material prevented the lateral dissipation of heat from the beaker to the surrounding air; thus, a uniform thermal gradient in a vertical plane was ensured. All experiments were conducted in a constant temperature room which was maintained at a temperature of 1° C. Each experiment was started when a salamander was placed on the top of the soil in the beaker which then was covered with a wire screen lid. The apparatus was placed in the dark portion of the cold room in such a fashion that light would not influence the behavior of the animals. After twelve to fifteen hours, the temperature was recorded at various depths in the soil; the animal was then recovered and its position in the beaker noted. For these tests a uniform soil moisture content was maintained throughout the soil in the beaker and in all individual experiments.

The water content of *Plethodon cinereus* was determined by the following method. First, the animal was washed to remove all foreign particles; secondly, it was dried by rolling the animal between pieces of paper toweling and weighed on an analytical balance; and lastly, it was dried in an oven to a constant weight and reweighed.

This procedure was followed on specimens the same day that they were collected and in this manner laboratory influences were not exerted on these animals. Specimens were collected at different seasons of the year from Tippecanoe and adjacent counties. The winter animals were recovered from the outdoor cages in Ross Biological Researve.

Results

Of the 51 *Plethodon cinereus* placed in the cages in November, 22 or 43% were retaken in February. Three of the original six *Eurycea bislineata* were recovered at the same time (Table I). No evidence was found as to the fate of the other specimens.

On February 22, 70% of the animals recovered were located eleven inches or deeper in the soil; on February 27, no specimens were found at that depth and only 20% of the animals were four inches or deeper in the soil. Obviously an upward vertical movement had occurred. During this five-day interval a marked increase in temperature was noted (Table II). Also an inversion of soil moisture relations had occurred. On February 22 the soil at a depth of 15 inches had a higher moisture content than at the surface, but

TABLE I. Results of hibernation studies on two species of salamanders.

a. February 22, 1951. Air temperature 6°C.

Number of specimens recovered	Species	Soil depth	Soil temperature	% soil moisture
3	[1]*P.c.*	at surface beneath leaf mold	4°C.	52
2	*P.c.*	11 inches	3°C.	86
1	[2]*E.b.*	11 inches	3°C.	82
2	*P.c.*	12 inches	3°C.	67
1	*E.b.*	14 inches	3°C.	73
1	*P.c.*	15 inches	3°C.	74

b. February 27, 1951. Air temperature 10.5°C.

Number of specimens recovered	Species	Soil depth	Soil temperature	% soil moisture
7	*P.c.*	at surface beneath leaf mold	8°C.	38
1	*E.b.*	at surface beneath leaf mold	8°C.	38
4	*P.c.*	1 inch	7°C.	40
1	*P.c.*	4 inches	5°C.	44
2	*P.c.*	9 inches	4°C.	30

[1]*Plethodon cinereus cinereus*
[2]*Eurycea bislineata bislineata*

on February 27 the surface soil contained more moisture than at a greater depth. Preceding February 22 heavy rains fell, thus accounting for higher soil moisture values on this date than on February 27.

Contrary to field observations of Blanchard (1933), these animals showed no tendency to aggregate during hibernation. It is noteworthy that the majority of the animals recovered were in close or direct contact with the screen; their usual position was with their backs against the wire. Perhaps this is an indication of a thigmotactic response by the animals. However, Test (1946) stated that *Plethodon cinereus* exhibited no dorsal thigmotaxis.

The hibernaculum of each specimen was found to be a hollowed-out cavity with smooth walls. The cavity was approximately two and one-half times as large as the animal; no entrance or exit to the hibernaculum was observed. Most of the animals were in a C-shaped posture, which seemed to be characteristic. No salamanders were found in the logs located in the cages. It would seem that logs were not a successful hibernating site for these

TABLE II. *Maximum and minimum air temperature (° C.) from February 22–27, 1951*

Date	Maximum temperature	Minimum temperature
February 22	6.0°	− 1.7°
February 23	11.0°	− 0.2°
February 24	14.0°	+ 0.6°
February 25	16.7°	+ 5.5°
February 26	14.4°	+10.0°
February 27	11.6°	+ 2.8°

TABLE III. *Reactions of* Eurycea bislineata bislineata *(Green) to a soil temperature gradient. Air temperature 1° C*

Experiment number	Soil temperature in ° C.	Depth of burrowing in cms
1	3.5	1.0
2	3.5	1.0
3	4.0	1.0
4	4.8	2.5
5	5.5	1.0
6	5.5	1.0
7	5.5	4.5
8	5.5	5.5
9	6.0	5.5
10	6.0	6.0

animals. No species differences were noted in any of the above observations.

In all laboratory experiments dealing with response of these animals to a soil-temperature gradient, the salamanders exhibited a decided response by burrowing in the soil in the direction of the higher temperature (Tables III, IV). To determine if these salamanders were responding to temperature and not merely demonstrating a burrowing response, a series of experiments was performed without establishing a temperature gradient. This was accomplished by allowing the temperature of the soil to come to equilibrium with room temperature and noting the position of the salamanders twelve hours later. They did not burrow under these conditions but remained at the surface. However, when the gradient was reestablished, without removing the animals, they did burrow. This clearly demonstrated their positive reaction to a soil-temperature gradient. A marked species difference could not be noted.

TABLE IV. *Reactions of* Plethodon cinereus cinereus *(Green) to a soil temperature gradient. Air temperature 1° C*

Experiment number	Soil temperature in ° C.	Depth of burrowing in cms
1	4.0	1.0
2	4.5	1.0
3	4.5	2.0
4	4.8	1.5
5	5.0	1.0
6	5.0	1.0
7	5.5	1.0
8	5.5	4.0
9	5.8	1.4
10	5.8	2.1

The water content of *Plethodon cinereus* at different seasons of the year is summarized in Table V. When comparing the water content of animals in the fall with that of winter animals, a significant difference of means was noted, t corresponding to $P = 0.001$. Unfortunately, the difficulty in obtaining specimens in the winter months of December and January did not permit a study of the water content during this period. Perhaps the loss of water would be even greater during this interval.

TABLE V. *Body weights (in grams) and water percentages of* Plethodon cinereus cinereus *(Green) at different seasons of the year*

Date	Original weight	Dry weight	Per cent water	Average % water
September 25, 1950	1.006	0.199	80.22	
	0.806	0.144	82.14	
	0.761	0.156	79.51	
	0.439	0.080	81.78	80.91
October 3, 1950	0.905	0.186	79.45	
	0.805	0.158	80.38	
	0.796	0.160	79.90	
	0.632	0.102	83.86	80.89
October 25, 1950	0.798	0.199	75.06	
	0.676	0.160	76.33	
	0.644	0.158	75.47	
	0.544	0.141	74.08	
	0.695	0.185	73.38	
	0.548	0.144	73.72	74.67
February 23, 1951	0.548	0.138	74.82	
	0.420	0.103	75.47	75.15
April 12, 1951	0.908	0.183	80.47	
	0.896	0.175	79.85	
	0.764	0.145	81.02	
	0.561	0.105	81.28	80.66
May 9, 1951	0.901	0.187	79.25	
	0.769	0.165	78.54	
	0.650	0.131	79.85	79.21
June 25, 1951	0.881	0.175	80.14	
	0.797	0.164	79.42	
	0.686	0.137	80.03	79.85

In May and late June the water content of this species is lower than in April, September, and early October. The reason for this slight variation is unknown.

No correlation between the size of the individual and per cent of body water was noted.

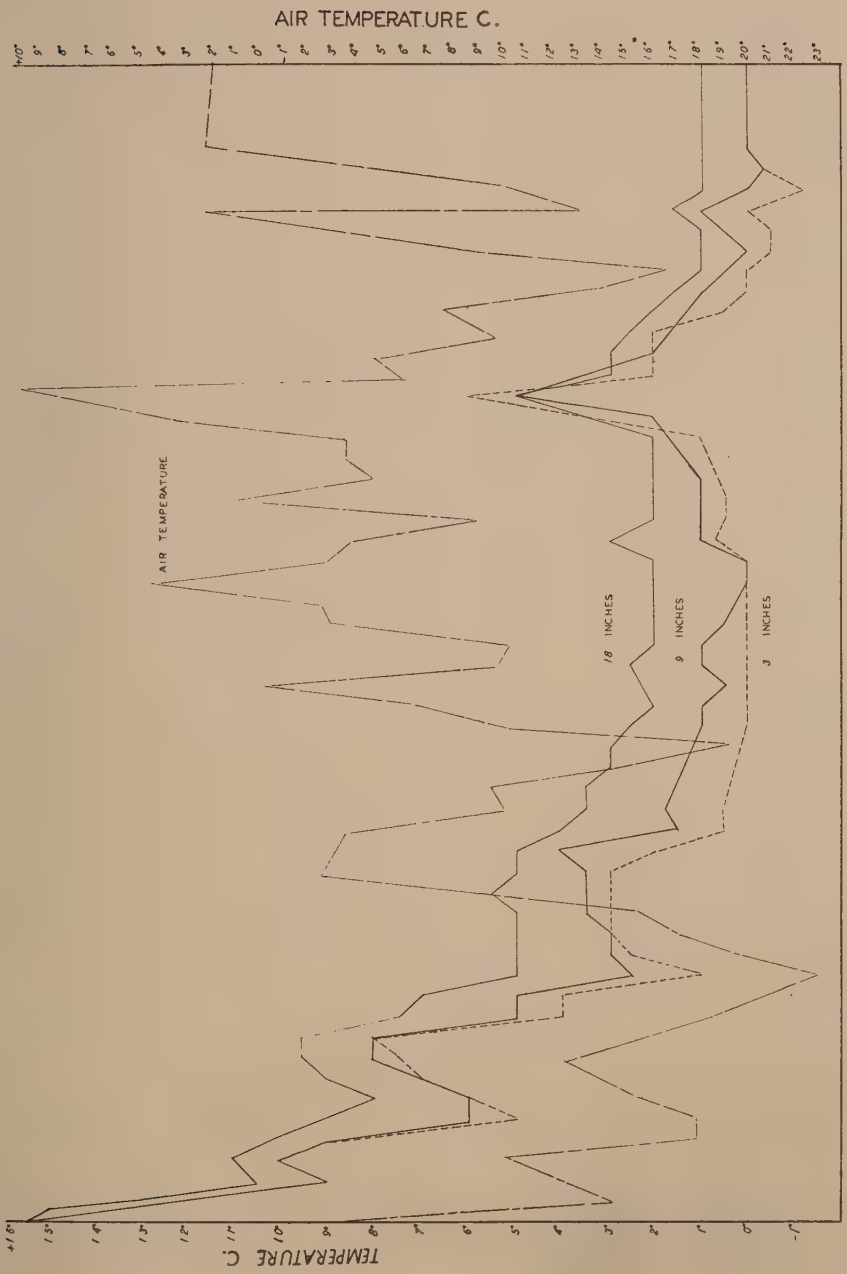

FIG. 1. Daily noon temperature at 3 levels in the soil and air temperature at Ross Biological Reserve, Indiana.

Discussion

In general, it appears that with the approach of winter, *Plethodon cinereus* and *Eurycea bislineata* move to a habitat in which they can best survive. Usually these animals are found at or near the surface of the soil in the warmer months, but as the temperature decreases in the fall they apparently burrow vertically deeper in the soil. In this manner they find a more stable environment in which to pass the winter. With the approach of spring, when the surface soil warms up, the animals move upward. At this time the animals begin to make their appearance in the leaf mold and under rocks or logs. The evidence in support of this generalized scheme is found in the field observations and experimental work of this study.

Temperature records taken at three different levels in the soil by Fitton and Brooks (1931) show that fall and spring temperature overturns occur in the soil. The concept of soil temperature overturn summarizes the facts that during the colder seasons of the year the deeper soil has a higher temperature than the surface soil and that, during the warmer months of the year, the temperature of the deeper soil is generally lower than the surface soil. In view of the influence of temperature on the metabolic activities of soil organisms, this principle has widespread application.

The climatic data obtained at Ross Reserve during the course of this study showed that if the air temperature was low for a considerable period of time, the soil temperature at a depth of nine inches was higher than the temperature recorded at the three inch level (Fig. 1). Most of the animals recovered on February 22 were deeper than nine inches and thus protected from the lower and more variable surface temperatures. The lowest temperature recorded at nine inches was 1° C. while at a depth of three inches the lowest temperature was − 1° C. Laboratory experiments show that when tested at low temperatures, these animals will burrow in the soil toward the warmer end of a soil temperature gradient.

Although the influence of temperature on these animals has been stressed in this paper, the importance of soil moisture must not be overlooked. An intimate relationship between the two environmental factors of temperature and moisture exists and they greatly influence each other. Shelford (1913) studied the response of *Plethodon cinereus* to gradients of evaporative power of the air and found that this species is very sensitive to dryness. Many other workers have noted the preference of salamanders for moist situations (Blanchard 1928; Cochran 1911; Hairston 1949).

On February 22, most of the animals recovered were eleven inches or deeper in the soil where the soil moisture was higher than at a depth of one inch. However, on February 27, when the majority of the animals were found within four inches of the soil surface, an inversion of soil moisture conditions had occurred and the soil above four inches in depth had a higher moisture level than at the greater depth. During the interval from February 22 to February 27, a warm period had occurred, melting the frozen topsoil.

It would seem that the stimulus for the upward spring movement of salamanders is a combination of a response to higher temperature and a change in soil moisture relationships. This condition accounts for the appearance of these animals at the surface of the forest floor throughout the spring and summer, except during prolonged hot, dry periods. Potzger (1939) observed in a study of the soil moisture content of a forest-covered slope that in summer the soil had a higher moisture content at the surface than at a depth of six inches.

From the results of the present investigation, it appears that the winter mortality of a population of salamanders is high. Approximately 50% of the original number of animals died during the course of

this study. It is possible that the mortality rate would be higher if the cages had not been opened until spring.

Only one explanation seems possible at this time as to why these animals stop at a certain depth in the soil. It has been noted that the greatest variation in soil temperature occurs in the uppermost inches of the topsoil; as the depth increases the temperature change is slight. For example, when testing the reactions of these animals to a soil temperature gradient, it was noted that a change of 3.5° C. occurred in the first ½ centimeter of soil, while only a 1.5° C. difference was found between the 1 centimeter and 6.5 centimeter levels. It appears, then, that as the animal penetrates deeper in the soil the temperature difference is decreased and the animal no longer responds. The time interval necessary for this process to take place in nature depends on the degree of thermal change. A gradual decrease in air temperature, as experienced with the approach of winter, may result in a slow rate of descent on the part of the animal. A sudden warm period of short duration during winter may cause members of these species to move upward in the soil as was observed in this study.

The hibernaculum of these animals, as described earlier, was very similar to that noted by Lathan (1918) for *Bufo fowleri.*

A seasonal difference in body water content can be observed in the case of the red-backed salamander and may be of adaptive value to this form, as has been demonstrated in the case of certain insects (Payne 1926).

Summary

Hibernation studies on two species of salamanders, *Plethodon cinereus cinereus* and *Eurycea bislineata bislineata,* were carried on by confining individuals of these species to a limited area in the soil by means of a wire barrier. Fifty-one specimens of *P. cinereus* and 6 *E. bislineata* were placed in this area at the beginning of November and the survivors were recovered later in the winter. The mortality for *P. cinereus* was 57% and for *E. bislineata* 50%.

On February 22, the first of these two cages was examined and 70% of the animals recovered were 11 to 15 inches in the soil where the temperature range was 3°–4° C. The second cage was inspected on February 27 and 80% of the specimens were within four inches of the topsoil. An upward vertical movement had presumably taken place. Weather data showed a marked increase in air temperature during this period and an inversion of soil moisture relationships.

The hibernaculum of both species was a hollowed-out cavity with smooth walls. The C-shaped posture of these animals seemed to be their characteristic hibernating pose.

Soil temperature and moisture influence hibernation. With the approach of winter, lowered soil temperature and/or adverse moisture conditions cause these animals to move downward in the soil. When these environmental conditions are reversed, the animals return to the surface of the soil.

When tested at low temperatures, these forms exhibited a preference for the warm end of a soil temperature gradient.

A seasonal difference was observed in the average percentage of water in the total body weight of *Plethodon cinereus.* The lowest value was found in the winter.

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BRUSH CONTROL IN SOUTHEASTERN NEW YORK: FIFTEEN YEARS OF STABLE TREE-LESS COMMUNITIES

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INTRODUCTION

The purpose of this paper is to report upon the vegetation of a tract of land 0.8 hectare (about 2 acres) in extent, involving a transect approximately 650 meters long (over 2000 feet) and over 12 meters wide (40 feet). It is part of a larger transect 64 kilometers (40 miles) long, in which brush control for fire-line purposes was effected by clearing and harrowing in 1934–1936. Although most of the line progressed to brush composed of tree species, the small part here described developed, coincidentally, to a complex of stable tree-less plant communities which has so far resisted reinvasion by unwanted woody plants. As a demonstration of relatively stable low plant covers that could be created today by selective application of herbicides, its description and interpretation is not only of academic interest, but of importance in the field of Plant Community Management where such covers are of practical value for many special purposes. This report is based in part on data from permanent plots, and in conjunction with other studies, is part of a long-term cooperative project between the Boy Scouts of America Greater New York Councils and the American Museum of Natural History.

The authors gratefully acknowledge the support of the above mentioned organizations in establishing this project. They also acknowledge information obtained from Professor Ralph Unger (Head, Department of Forest Extension, State University of New York Forestry College, Syracuse) who directed the activities in 1934–1936, and from Mr. Kenneth Crandall, Property Superintendent, Ten Mile River Scout Camps, Narrowsburg, New York, resident on the area at that time. Mr. A. H. Whitney, Assistant Director, New York State Science Service, Albany, kindly supplied references and information on the geology of the region. The field data here published were obtained by the authors during the period August 30–September 1, 1951.

The transect described is part of the boundary fire line of the Ten Mile River Scout Camps, owned by the Greater New York Councils, Boy Scouts of America. This 12,000 acre tract is in southeastern Sullivan County, southeastern New York. The part here reported upon lies in southern Bethel Township, about 1 kilometer north and east of Crystal Lake.

The geological substructure of this entire region is the Catskill formation of Upper Devonian age, comprising freshwater piedmont and delta deposits, mainly sandstones but also shales and conglomerates. Locally, the material is a grayish sandstone. These are overlain by highly variable glacial deposits, the weathering of which has given rise to the present soils. On the transect, two soils have been mapped by Secor *et al.* (1946): Lackawanna stony silt loam shallow phase and Norwich stony silt loam, both fourth-grade soils. The Lackawanna is that of well-drained uplands, from which bedrock outcrops on the summits, and which varies from being exceedingly stony and shallow on the steeper slopes to conditions on the lower slopes that approach the non-stony first-grade Lackawanna silt loam. The Norwich stony silt loam is that of the poorly drained flatlands near the small

streams, occasionally so covered by organic debris that no stones are visible. Elevations on the transect vary from 1260 to 1380 ft. above sea level.

The nearest Weather Bureau station is at Jeffersonville, 12 miles north, elevation 1240 ft., and the following data were obtained from the U. S. Weather Bureau Climatic Summary (1935). The local climate is continental in type, varying with elevation above sea level. The average length of the growing season, based on records of 27 years, is from May 20th to September 27th, a total of 130 days. Average monthly temperatures in °F, based on 27 years, are as follows for January to December respectively: 22.8, 22.3, 32.7, 44.9, 55.3, 63.3, 67.9, 65.7, 60.1, 49.2, 37.2 and 26.2. Average monthly precipitation, in inches, based on 27 years, are as follows for January to December respectively: 2.87, 2.84, 2.95, 3.36, 3.17, 3.70, 4.54, 4.72, 3.69, 3.46, 2.95, 2.93, with a total annual precipitation of 41.18 inches.

In the general upland of the region, the above-mentioned factors have interacted to form a relatively small number of basic site-types, varying from rock outcrops on the summits to aquatic sites of streams, lakes and bogs. The major plant communities are distributed in obvious relation to these site types. Black spruce (*Picea mariana*),[1] red spruce (*Picea rubens*), *Chamaedaphne* and its customary associates are found in the bogs. Alder (*Alnus rugosa*), *Typha latifolia,* and such herbs as *Lobelia cardinalis* and *Chelone glabra* occur along lake shores and stream banks. Poorly drained inorganic soils at the heads of lakes and adjacent deep-soiled lower slopes are covered with forests of hemlock (*Tsuga canadensis*), sometimes pure, often mixed with yellow birch (*Betula lutea*). Beech (*Fagus grandifolia*) is sporadic, but common where found. In other instances, forests apparently on the same site-type are predominantly red maple (*Acer rubrum*) and white pine (*Pinus strobus*). In general these footslope forests are typical of the upland forests farther north, often known as the "hemlock-northern hardwoods type."

The predominant type of the region, that of the stony upper slopes and rolling upland soils, is a dry oak forest in which white oak (*Quercus alba*), black oak (*Quercus velutina*) and chestnut oak (*Quercus prinus*) predominate. Species present in a minority include: *Carya ovata, Amelanchier* sp., *Pinus strobus*, pitch pine (*Pinus rigida*), *Prunus serotina, Quercus coccinea, Quercus ilicifolia, Quercus rubra, Fraxinus americana, Betula populifolia, Betula lenta, Acer rubrum, Populus tremuloides, Castanea dentata, Carpinus caroliniana, Ostrya virginiana, Sassafras albidum, Populus grandidentata, Hamamelis virginiana,* and *Crataegus* sp. *Kalmia latifolia* is by far the most abundant shrub, and forms a continuous stand under much of the forest, although locally it is absent and the forest floor is all but bare. Other shrubs that are frequent to common are: *Vaccinium corymbosum, Viburnum* sp., *Lyonia ligustrina, Vaccinium vacillans, Vaccinium angustifolium, Gaylussacia baccata, Kalmia angustifolia, Comptonia peregrina, Spiraea tomentosa,* and *Spiraea latifolia. Lycopodium obscurum, Lycopodium complanatum, Pteridium aquilinum, Dennstaedtia punctilobula,* and *Onoclea sensibilis* are locally common. The lumbering history of the region indicates that large quantities of both pitch pine and white pine have been removed in past decades and one must acknowledge the fact that the forest in the days of early white settlement must have been of completely different physiognomy, and in turn must have arisen in Indian times under circumstances—possibly with frequent fires playing a role—which no longer exist. There is no evidence at this time of any developmental trend within the forest: the oak trees are growing slowly and reproduction of any kind is negligible.

[1] Latin names of plants are those of Fernald (1950).

Conversion: 1934–1936

As concepts of value in the field of Vegetation Management,[2] where relatively stable communities of new kinds are wished, the junior author has used the ideas of "Conversion" and of "Maintenance" (Egler 1949, 1951a, 1951b).

Conversion involves the operational procedures concerned with removing or otherwise eliminating the unwanted species of plants. This matter involves not only root-killing the larger individuals that are highly conspicuous, but rendering ineffective the seedlings, seeds, rhizomes, or other propagules that may be in or on the soil.

Maintenance is the subsequent management process concerned with the removal or other control of unwanted species that *re*invade from outside the area, and develop successfully. Such reinvasion can occur either peripherally (as by rhizomes or runners), or scatteringly (as by windblown seed).

The mechanical Conversion process on the transect under study is admittedly one which cannot be repeated today at reasonable cost. Its botanical terminal effects however can, in the opinion of the authors, be duplicated by newer and cheaper herbicidal "tools." Since these tools did not exist in the 1930's, the present transect can be used as a demonstration of probable Maintenance costs on this type of land 15 years after successful Conversion with the chemical "tools" available today. Such chemical Conversion is now in progress on all other parts of the 40 miles of fire lines.

In December, 1933, a Civilian Conservation Corps camp was established on the Ten Mile River tract, and in the fall of 1934 the initial clearing of the 40 miles of fire lines was begun. Trees were chopped down, cut into lengths and hauled out for camp fuel, except in the more isolated regions. Here the logs were removed by the local populace in the years immediately following. Stumps were blasted, pulled, and then dragged off by cable and tractor and left at the margins. Shrubs such as laurels and tall blueberries were not only cut down, but the roots were ripped out by a large spike-toothed "A" frame harrow. No bulldozer was used and the original top soil is still in place. As a final procedure, the heavy spike-tooth harrow was repeatedly dragged over the line wherever outcropping bedrock ledges did not interfere. It was the plan to repeat this process at least once a year, with the intent of maintaining a smooth right of way of bare soil completely devoid of all plant life.

The C.C.C. camp left the region in September, 1936, and no harrowing or any other operations have been carried out on the fire line in the 15 years succeeding. In the first years after 1936, grasses appeared to predominate. After that, shrubs and trees developed in varying densities, so that the present vegetation on the 40 miles is composed of a great variety of herb, shrub, and tree communities.

In the light of present botanical conditions, it is inferred that this variation in tree growth is due directly to coincidences in the distribution of propagules of different species at the time of and shortly after abandonment, and not to varying physical operations on the land. In some sections, light-seeded species such as birch and aspen were able to gain a foothold and maintain themselves, although no significant quantity has come in since. Oaks and hickories, with heavy seeds that do not migrate far except by action of small mammals, give only local indication of having produced a heavy crop, such as would have been planted in part by the harrowing process, with an appreciable number of survivors at the present time. On rocky sites, root systems were apparently left in the soil, and these places now show some of the densest brush. On other sites, root-suckering species such as blackberry and sumac were favored by the mechanical operations, since apparently the sections of

[2] It is not the usual policy of this journal to capitalize common nouns such as "ecology," "forest management," etc. "Vegetation Management," "Conversion," "Abundance," etc., are capitalized in this paper at the special request of the authors.—Bot. Ed.

roots remaining in the land could survive to grow. Laurel, known to extend its area in the forest by layering, has not extended appreciably into the fire line.

Very locally, and apparently by factors of coincidence and chance, non-tree vegetation prevails. Original root systems of the trees did not survive. In addition, neither light- nor heavy-seeded species gained an entry on the bare soil. Root-suckering trees such as sassafras and aspen, were not present. In such rare instances, the omnipresent rhizomatous and root-suckering grasses, ferns, and low shrubs were probably favored by the harrowing process, since the severing of underground parts seemingly stimulates shoot production. It would appear that on the abandonment in 1936 of these areas, a low plant community came into existence which has not yet been successfully invaded by trees. A description of this vegetation is the main purpose of this report.

The Adjacent Forest: 1951

The adjacent forest was sampled at intervals of 27.3 meters (about 89.6 ft.). This interval was chosen so that there would be three samples adjacent to each 0.1-hectare plot described below. The samples were taken the entire length of the 650 meter transect, on the "inner" side, i.e., on Boy Scouts of America property. Each was a circular plot about 10 meters in radius. For each plot, the trees were listed in terms of three degrees of Predominance: C (common), F (frequent), and R (rare). Shrub and herb layers were noticed, but not recorded, for in composition they did not differ signifi-

Table I. *The black oak-white oak forest; floristic composition and Abundance of the tree canopy, based on 11 plots taken at regular intervals along the transect: A—abundant, C—common, F—frequent, R—rare.*[3] *Species are included which, though not in the plots, occur in the vicinity*

Species	Abundance (in numbered plots)											Constancy
	1	2	3	4	5	6	20	21	22	23	24	
Acer rubrum	F	F	F	R	F	C	F	C	C	C	C	11
Acer spicatum												—
Amelanchier sp.		R		F	F	R	F	R	R	F		8
Betula lenta												—
Betula lutea					R	C		R				3
Betula populifolia				R	R		R					3
Carya ovata												—
Castanea dentata	R											1
Crataegus sp.											R	1
Fagus grandifolia												—
Fraxinus americana											R	1
Fraxinus nigra												—
Hamamelis virginiana		R		R		R	R			F	F	6
Pinus rigida	F								R			2
Pinus strobus							R	R		R		3
Populus grandidentata		F		F	R			R		R		5
Populus tremuloides	R						F	R	R		R	5
Prunus serotina												—
Quercus alba	C	C		F	R	R	R		C	R	R	9
Quercus ilicifolia						R						1
Quercus montana	R	F	F	F		R						5
Quercus coccinea							R		R	R		3
Quercus rubra												—
Quercus velutina	R	F	F			R	F	F	C	C	R	9
Sassafras variifolium		R										1
Tsuga canadensis					F	F		F				3

[3] Constancy is expressed as the total number of plots in which a species is found (regardless of its Abundance). With this number as numerator, and the total number of plots as denominator (here, 11), the fraction allows comparison with data in other tables.

TABLE II. *The hemlock-yellow birch forest of poorly drained flats and adjacent gentle slopes. Floristic composition and estimated Abundance of the tree canopy, based on 13 plots taken at regular intervals along the transect*

Species	Abundance (in numbered plots)													Constancy
	7	8	9	10	11	12	13	14	15	16	17	18	19	
Acer rubrum	R	F	F	F		C	C	C	C	R	C	F	R	13
Acer spicatum		R												1
Amelanchier sp.			R	R					R	C		R		5
Betula lenta														—
Betula lutea	R	F	F	F	C	C	C	R	R	R		R	F	12
Betula populifolia									R	C				2
Carya ovata														—
Castanea dentata														—
Crataegus sp.														—
Fagus grandifolia														—
Fraxinus americana														—
Fraxinus nigra		R			R	R								3
Hamamelis virginiana					F		R	R	F		R			5
Pinus rigida						F		R			F			3
Pinus strobus	R	R										R	R	4
Populus grandidentata										R		R		2
Populus tremuloides			R	C	R				C		C		R	6
Prunus serotina								R						1
Quercus alba												R		1
Quercus ilicifolia														—
Quercus montana										R				1
Quercus coccinea														—
Quercus rubra														—
Quercus velutina	R				R		R	R						4
Sassafras variifolium														—
Tsuga canadensis	C	C	C	C	C	C	C	F	R		C	C	C	12

cantly from that of the transect itself. The data indicate that for present purposes, only two forest communities need be recognized: a black oak-white oak forest, and a hemlock-yellow birch forest. Red maple is common in both types.

The black oak-white oak forest

Black oak and white oak are the two commonest character trees of the upland forest as sampled (Table I), with chestnut oak becoming more frequent on the upper slopes. *Acer rubrum* is extremely common, although the nature of the forest is very different from that of the lower slopes where *Acer* is also present. Both *Populus tremuloides* and *P. grandidentata* occur very sporadically, but may be frequent or common where they do occur. *Amelanchier* and *Hamamelis virginiana* are generally distributed, and may predominate where oaks are sparse. White pine, the most desired timber tree, is infrequent, and gives no evidence of increasing in number.

The hemlock-yellow birch forest

The forest of poorly drained soils and adjacent gentle slopes is physiognomically conspicuous because of the great density of hemlock (Table II), and the characteristically open understory. Actually, *Acer rubrum* is also common, although its basal area is considerably less. Yellow birch is highly characteristic of these low sites, and ranks third in importance. Black ash (*Fraxinus nigra*) is the only other indicator species; other trees are indifferent in their site tolerances.

FIRE LINE VEGETATION: 1951

The vegetation of this part of the fire lines was studied by means of plots of three different sizes: 0.1 hectare; 100 sq. m.; and 0.5 sq. m.

FIG. 1. View looking north through the black oak-white oak forest, showing a 15-year-old ground cover in which *Comptonia, Vaccinium,* and *Gaylussacia* are predominant.

The 650 m. long transect was divided into 8 permanent 0.1-hectare units, each 82 m. long and 12.2 m. wide. Data from these plots included the Coverage of tree and low-shrub-and-herb layers, the floristic composition of each, and the relative Coverages of the predominant species.

Photographs have been taken, in both directions along the fire line, from permanent stations at the ends of these tenth-hectare plots (Fig. 1).

Permanent 10-meter-square plots are located at one end of the tenth-hectare units. On each such plot, floristic composition and estimated Coverages are recorded in more detail. These plots will not be mentioned further in this report.

Temporary ± 0.5 square meter quadrats were laid out in pure stands of the 10 species that were most predominant in the vegetation. Although such pure communities are areally in the minority,

they form the most suitable "standards" by which to gauge the endless variety of intermixtures of these species, and to interpret the status of such mixtures in the total vegetation.

The Comptonia-Dennstaedtia community

On the well-drained upland soils, a single herb and low shrub community is considered to exist, replacing the regional black oak-white oak forest (Table III). It also occurs on the lower slopes on hemlock and yellow birch land, where the drainage is not such as to allow a cover of sphagnum to develop. Large tree shoots are very few; they appear mainly to be from old root systems, and probably date back to the years preceding 1936.

Kalmia latifolia, Lyonia ligustrina, and *Vaccinium corymbosum* are shrubs reaching heights of 0.5–1.0 m., and as such could form a stratum of their own, undesirable for purposes of the fire line. On the transect studied, however, these three shrubs were so sparsely distributed that they would not interfere with truck transportation at times of emergency.

The predominant vegetation is a cover of low shrubs and herbs averaging one-half meter in height, in which only 6 species form over 90 per cent of the vegetation: *Comptonia peregrina* and *Dennstaedtia punctilobula* are the most abundant. *Dryopteris noveboracensis* forms a close third. *Vaccinium angustifolium, Gaylussacia baccata,* and *Kalmia angustifolia* follow in that order of abundance. *Polytrichum commune* often occurs as a ground cover, with Lycopodiums. The remaining species appear in the interstices where these predominants happen to be absent. Although, on first glance, the vegetation appears to be a mosaic of these six predominants, on closer inspection it is seen that they occur in all degrees of mixture, sometimes segregating into two levels, as, for example, where *Vaccinium angustifolium* forms a stratum below *Comptonia.*

Tree seedlings do occur in this vegetation, though they are all but invisible ex-

TABLE III. *The Comptonia-Dennstaedtia community, on well-drained slopes, with either deep soil or thin stony soil. Lackawanna stony silt loam. Elevation: 1260–1380 ft. Equivalent forest types: black oak-white oak forest, and higher parts of the hemlock-yellow birch forest. Data obtained from 0.1 hectare plots. Species found only in the 0.5 sq. m. plots not included*

AC	V	
Unwanted brush stratum (over 5 ft.). Coverage less than 1%. (Restricted to upper rocky slopes, except for the alder on a streambank.)		
+	3	*Acer rubrum*
+	3	*Alnus rugosa*
+	3	*Betula lenta*
+	3	*Quercus alba*
+	3	*Quercus montana*
Herb and low shrub stratum. Coverage 100%		
1	2	*Anaphalis margaritacea*
1	2	*Aralia nudicaulis*
+	+	*Bromus ciliatus*
2	2	*Carex* sp. (low; sterile)
3	3	*Comptonia peregrina*
3	3	*Dennstaedtia punctilobula*
+	+	*Diervilla lonicera*
3	3	*Dryopteris noveboracensis*
1	3	*Gaylussacia baccata*
1	3	*Kalmia angustifolia*
+	3	*Kalmia latifolia*
+	+	*Lycopus* sp.
+	3	*Lyonia ligustrina*
+	+	*Lysimachia quadrifolia*
1	3	*Osmunda cinnamomea*
3	2	*Polytrichum commune*
1	2	*Pteridium aquilinum*
1	2	*Panicum* spp.
1	2	*Rubus hispidus*
1	2	*Rubus* (*allegheniensis* type)
1	2	*Rubus idaeus*
1	2	*Spiraea latifolia*
1	2	*Spiraea tomentosa*
1	2	*Solidago graminifolia*
+	+	*Spiranthes* sp.
+	3	*Vaccinium corymbosum*
2	3	*Vaccinium angustifolium*
+	+	*Vaccinium vacillans*
+	+	*Acer rubrum*
+	+	*Betula populifolia*
+	+	*Hamamelis virginiana*
+	+	*Quercus alba*
+	+	*Quercus velutina*
+	+(1)	*Pinus strobus*
+	+	*Tsuga canadensis*
+	+	*Populus tremuloides*

AC—Abundance and Cover, combined: +—sparsely or very sparsely present; 1—plentiful but of small cover value; 2—numerous, covering at least 1/20 of the area; 3—covering $\frac{1}{4}$ to $\frac{1}{2}$ of the area; 4—covering $\frac{1}{2}$ to $\frac{3}{4}$ of the area; 5—covering more than $\frac{3}{4}$ of the area. V—Vitality: +—growth extremely feeble, plant barely surviving; 1—growth obviously poor; 2—growth average, reproduction poor; 3—growth and reproduction good.

cept on close inspection. *Acer, Betula, Hamamelis,* oaks, pines, hemlock, and *Populus* are all to be found. Their size and form, however, is highly significant. Almost always they are less than 15 cm. tall, spindly and poorly developed under the canopy of ferns and low shrubs, sometimes decumbent under the mat of fallen and decayed vegetation, and always giving evidence of having repeatedly died back, or having been cut back by rodents or mammals. They give no evidence of being the progenitors of a future forest.

The six predominant species of low shrubs and ferns, even though commonly occurring in mixture, differ in their degrees and kinds of phytosociological dominance, and consequently the more important pure phases were studied by means of arbitrarily chosen 0.5 sq. m. sample plots. Considering the superficial "purity" of each, the large number of species found is surprising. Even more surprising is the universally very low Vitality shown by all these accompanying plants. They are as feeble and depauperate as the tree seedlings mentioned above and in many cases cannot be identified as to species. With this feature exemplified in both tree seedlings and herbs, one is led to have considerable respect for the ability of these plants to "hold their own" against all other invading species.

The Comptonia phase.—Comptonia is the most "open" in growth of these predominant species, and this characteristic is shown not only by its almost constant admixture with other plants but with the large floristic composition of the type. The following data are based on 10 sample plots. Symbols for AC and V are defined in Table III. P, Presence in per cent, is based on the proportional number of plots in which a species occurred.

AC	V	P	
5	3	100	*Comptonia peregrina*
+	+	10	*Anaphalis margaritacea*
+	+	10	*Bromus ciliatus*
+	+	10	*Calamagrostis cinnoides*
+	+	30	*Carex* sp. (broad-leaved)
+	+	20	*Carex* sp. (narrow-leaved)
+	+	20	*Cornus canadensis*
+	+	10	*Desmodium* sp.
+	+	10	*Diervilla lonicera*
+	+	20	*Gaultheria procumbens*
+	+	40	*Hamamelis virginiana*
2	1	20	*Kalmia angustifolia*
+	+	20	*Kalmia latifolia*
+	+	10	*Maianthemum canadense*
+	+	10	*Osmunda cinnamomea*
+	+	10	*Polygala paucifolia*
+	+	60	*Polytrichum commune*
+	+	30	*Potentilla canadensis*
+	+	80	*Panicum* spp.
+	+	20	*Quercus velutina*
+	+	10	*Ranunculus acris*
+	+	90	*Rubus hispidus*
+	+	50	*Rubus* sp. (erect)
+	+	10	*Sassafras albidum*
+	+	40	*Solidago rugosa*
+	+	20	*Spiraea latifolia*
+	+	10	*Spiraea tomentosa*
2	1	70	*Vaccinium angustifolium*
+	+	60	*Viola* sp.

The Dennstaedtia phase.—Patches of *Dennstaedtia* give the appearance of being much more "closed" and dense than the stands of *Comptonia.* An undercover of *Vaccinium angustifolium,* e.g., is never found below it. Each year the foliage drops completely to the ground, and though the number of other species present is considerable, they are all of extremely low Vitality. The following data are based on ten sample plots.

AC	V	P	
5	3	100	*Dennstaedtia punctilobula*
+	+	20	*Acer rubrum*
+	+	10	*Antennaria* sp.
+	+	10	*Aster acuminatus*
+	+	30	*Aster* sp.
+	+	10	*Betula lutea*
+	+	10	*Betula populifolia*
+	+	10	*Botrychium* sp.
+	+	20	*Calamagrostis cinnoides*
+	+	10	*Coptis trifolia*
+	+	20	*Cornus canadensis*
+	+	10	*Cypripedium acaule*

AC	V	P	
+	+	20	*Diervilla lonicera*
+	+	10	*Fragaria* sp.
+	+	20	*Hamamelis virginiana*
+	+	20	*Hieracium* sp.
+	+	10	*Hydrocotyle americana*
+	+	20	*Impatiens* sp.
+	+	20	*Kalmia angustifolia*
+	+	20	*Kalmia latifolia*
+	+	20	*Lycopodium obscurum*
+	+	20	*Mentha* sp.
+	+	30	*Maianthemum canadense*
+	+	20	*Mitchella repens*
+	+	10	*Oxalis* sp.
+	+	30	*Panicum* spp.
+	+	90	*Polytrichum commune*
+	+	40	*Potentilla canadensis*
+	+	10	*Ranunculus acris*
+	+	80	*Rubus hispidus*
+	+	50	*Rubus* sp. (erect)
+	+	10	*Solidago rugosa*
+	+	10	*Spiraea tomentosa*
+	+	20	*Tsuga canadensis*
+	+	30	*Trientalis americana*
+	+	30	*Vaccinium angustifolium*
+	+	80	*Viola* sp.

The Dryopteris phase.—Colonies of the New York fern are very similar in general appearance to those of *Dennstaedtia,* and the two ferns are very commonly intermingled. There are some indications that this fern can tolerate lower and moister conditions than the other predominants of the *Comptonia-Dennstaedtia* community, and thus tends to form a belt of its own at the higher margins of the undrained lowlands. The following data are based on nine sample plots, several of which were sufficiently low to have sphagnum as a ground cover.

AC	V	P	
5	3	100	*Dryopteris noveboracensis*
+	+	11	*Antennaria* sp.
+	+	11	*Aster acuminatus*
+	+	11	*Aster* sp.
+	+	11	*Betula lutea*
+	+	11	*Clintonia borealis*
+	+	11	*Coptis trifolia*
+	+	11	*Cornus canadensis*
+	+	44	*Calamagrostis cinnoides*
+	+	22	*Desmodium* sp.
+	+	11	*Equisetum sylvaticum*
+	+	11	*Fragaria* sp.
+	+	11	*Gaultheria procumbens*
+	+	11	*Hamamelis virginiana*
+	+	11	*Hydrocotyle americana*
+	+	11	*Kalmia angustifolia*
+	+	11	*Kalmia latifolia*
+	+	11	*Mentha* sp.
+	+	33	*Maianthemum canadense*
+	+	22	*Mitchella repens*
+	+	11	*Onoclea sensibilis*
+	+	11	*Osmunda cinnamomea*
+	+	22	*Panicum* sp.
+	+	66	*Polytrichum commune*
+	+	11	*Populus tremuloides*
+	+	33	*Potentilla canadensis*
+	+	55	*Rubus hispidus*
+	+	44	*Sphagnum* sp.
+	+	11	*Spiraea tomentosa*
+	+	11	*Tiarella cordifolia*
+	+	33	*Tsuga canadensis*
+	+	11	*Vaccinium angustifolium*
+	+	55	*Viola* sp.

The Vaccinium angustifolium phase.—As judged by 7 sample plots, the number of species found, and the low condition of their Vitality, *Vaccinium angustifolium* forms the densest cover of the 6 species here considered predominant. One of the plots had no other plants whatever in it, and the other showed such a dense matting of decumbent branches and old leaves, as well as a complete canopy of foliage, that the observed stability of this cover type in other regions does not seem unreasonable. Plot data are as follows:

AC	V	P	
5	3	100	*Vaccinium angustifolium*
+	+	14	*Acer rubrum*
+	+	57	*Cornus canadensis*
+	+	14	*Calamagrostis cinnoides*
+	+	29	*Gaultheria procumbens*
+	+	14	*Lycopodium obscurum*
+	+	14	*Maianthemum canadense*
+	+	14	*Medeola virginica*
+	+	29	*Polygala paucifolia*

AC	V	P	
+	+	57	*Polytrichum canadense*
+	+	14	*Potentilla canadensis*
+	+	71	*Rubus hispidus*
+	+	14	*Viola* sp.

The Gaylussacia phase.—Huckleberry is not common as a pure type on the transect studied; only two 0.5 sq. m. plots were sampled. These showed the community as being less dense than that of *Vaccinium augustifolium,* but more dense than that of *Comptonia peregrina.* It is obviously a community that can successfully retard the invasion of the land by tree seedlings.

The Kalmia angustifolia phase.—Pure stands of sheep laurel occur about as frequently as do those of huckleberry. On the basis of two samples of this evergreen type, it appears that its floristic composition is low, and approaches that of the *Vaccinium angustifolium* phase. It is apparently a type which is extremely resistant to successful invasion by trees.

The Carex crinita–Calamagrostis cinnoides community

On poorly drained lowland soils, for present purposes a single herbaceous community is considered to exist, replacing the hemlock-yellow birch forest. It occurs on an aggregate of only 15 per cent of the total transect. At its lower margin, with a higher water table, *Typha latifolia* and *Alnus incana* appear. At its upper margins, it passes rather abruptly into the *Comptonia-Dennstaedtia* community above described, often with *Dryopteris noveboracensis* predominant. The division between the two is at a lower elevation, however, than for their corresponding forest types: the hemlock-yellow birch forest advances up the lower slopes, whereas the *Carex-Calamagrostis* community is completely restricted to the poorly drained areas.

Carex crinita and *Calamagrostis cinnoides* together make up probably over 85 per cent of the mass of the vegetation (Table IV). *Scirpus cyperinus* appears conspicuously in a few small spots. An under-stratum of *Sphagnum* species blankets the entire land, covering the inorganic soil and possibly contributing significantly to the layer of organic material usually present. In about half the area covered by this community, *Polygonum sagittatum* is extremely abundant, growing through and among the herbaceous plants, and giving a superficial appearance of there being an entirely different plant community. Careful observation, however, indicated that the *Polygonum* was only an addition to the community and did not affect the manner of occurrence of the other species: no other differences were found which would warrant a segregation of the plant associa-

TABLE IV. *The Carex crinita–Calamagrostis cinnoides community, on flat poorly drained inorganic soils, covered by 1–3 inches of organic material. Lackawanna stony silt loam. Elevation: 1260–1300 feet. Equivalent forest type: hemlock-yellow birch forest. Data obtained from 0.1 hectare and seven 0.5 sq. m. plots*

Unwanted brush stratum (over 5 ft.). Coverage 0%. (A few alders along a stream bank are not considered a part of this community.)

Herb stratum. Coverage 100%

AC	V	
4	3	*Carex crinita*
4	3	*Calamagrostis cinnoides*
1	2	*Anaphalis margaritacea*
+	+	*Aster* sp.
+	+	*Betula lenta*
+	+	*Betula populifolia*
1	2	*Dennstaedtia punctilobula*
1	2	*Dryopteris noveboracense*
1	1	*Equisetum sylvaticum*
+	+	*Hamamelis virginiana*
+	+	*Hydrocotyle americana*
+	+	*Impatiens* sp.
1	2	*Kalmia angustifolia*
+	+	*Lysimachia quadrifolia*
+	+	*Mentha* sp.
1	2	*Onoclea sensibilis*
1	3	*Osmunda cinnamomea*
+	+	*Pinus strobus*
3	3	*Polygonum sagittatum*
1	2	*Rubus hispidus*
+	+	*Rubus* sp. (erect)
2	3	*Scirpus cyperinus*
1	2	*Solidago graminifolia*
5	3	*Sphagnum spp.*
1	2	*Spiraea tomentosa*
+	+	*Trientalis americana*
+	+	*Tsuga canadensis*
+	+	*Viola* sp.

tion. Other species occurred sporadically; and those marked "+" in the table were all feeble individuals of low Vitality. Tree seedlings were infrequent. It would appear that a few should eventually develop into trees, but at least in the past 15 years none have so developed. Those seedlings found were small slender plants, giving evidence of being browsed or nipped by animals, and of being weighted down in the autumn by the falling herbaceous material.

Maintenance: Post–1951

From the standpoint of a fire line vegetation covered with low plants and suitable for use as a truck trail in times of emergency, the present *Comptonia-Dennstaedtia* and *Carex-Calamagrostis* communities, in existence for 15 years without any cutting or other treatment, are not now in need of thinning operations because of invaded trees. It is not assumed that these communities will remain indefinitely free of tree growth, for tree seedlings are present, and in one section about a dozen pines have terminal buds now above the level of the lesser vegetation (in itself not proof that they will continue to grow). Unfortunately, no published research is known to the authors which can be brought to bear in indicating the future stability of these communities. As judged on the basis of the extreme density of these low covers, the feeble growth of the associated species, the indication of constant rodent and mammal damage, and the effects of blanketing in autumn with dead vegetation, there are no indications at this time that invading trees will be more successful in the coming 15 years than they have been since 1936.

Summary

A transect, 650 meters long and 12 meters wide, was studied for floristic composition and structure of the plant communities, in a region with upland forests of black oak and white oak, and hemlock and yellow birch on the flats. The area is part of a fire line on a 12,000 acre tract owned by the Boy Scouts of America, and was cleared by a Civilian Conservation Corps in 1934–1936. Operations included spike-harrowing the area. On the line here described, the accidental absence of suitable conditions for germination and development of tree seeds and the absence of root-suckering trees allowed the formation of a dense low vegetation that has since prevented the mass invasion of trees. Such trees as have invaded now have a Coverage of less than 1 per cent. The transect was divided into permanent 0.1 hectare units, each with a permanent 10 sq. m. plot. On the basis of these, and temporary 0.5 sq. m. plots, two plant communities were recognized; a *Comptonia-Dennstaedtia* community and a community of *Carex crinita* and *Calamagrostis cinnoides*. In the former, *Dryopteris noveboracensis, Vaccinium angustifolium, Gaylussacia baccata,* and *Kalmia angustifolia* were also predominant; in the latter, *Scripus cyperinus*. Over 50 other species of plants were found, the majority of which occurred in a very low state of Vitality. Tree seedlings are occasional, but with very few exceptions the individuals are small, feeble, and give evidence of being repeatedly cut back by animals and matted down by falling vegetation. At the present time, there are no indications that trees will be any more successful in invading in the next 15 years than they were in the past 15 years.

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A STUDY OF HIBERNACULA AND HIBERNATING ASSOCIATIONS OF SNAKES AND AMPHIBIANS IN MICHIGAN

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During the course of ecological studies of a garter snake population near Dixboro, Washtenaw County, Michigan from 1948 through 1951, many data were recorded on hibernating snakes. The 50-acre area concerned surrounds and includes a button-bush marsh, with a mixed growth of sumac and grasses to the north and west, to the east a grazed pasture and to the south an oak-hickory wood lot. The grass-sumac area, which has a south-facing hillside with a flat area between it and the marsh, showed definite concentrations of snakes in the spring and fall.

ANT MOUND

It was on this flat area that the first signs of hibernating activity were observed on October 6, 1948, when two recently born common garter snakes (*Thamnophis s. sirtalis*) were recorded near an abandoned ant mound. Subsequent observations definitely proved this mound to be a hibernaculum for a large number of individuals representing a variety of species of snakes and amphibians.

The circular ant mound, which was two feet in diameter and extended about six inches above the surrounding ground level, lay at the base of the gentle south-facing slope 75 feet from the marsh. Weeds, lichens, and mosses were growing on and about the mound. Numerous small entrances from ¼ to 1 inch in diameter led to small tunnels within the mound.

On three other occasions between the first observation and the following November 11, young-of-the-year common garter snakes and ribbon snakes (*Thamnophis s. sauritus*) were recorded sunning themselves at this ant mound. One of the common garter snakes had previously been recorded here.

The activity near this ant mound was followed throughout 1949, and during this period snakes were associated with it at least three times during the spring and three times in the fall. In the spring, 17 were ribbon snakes, one a common garter snake, one a Butler's garter snake (*Thamnophis butleri*) and one a Dekay's snake (*Storeria dekayi*). All had been born the previous summer. Those observed in the fall were: one adult common garter snake, one small common garter snake, one ribbon snake, one Butler's garter snake, and one smooth green snake (*Opheodrys v. vernalis*); all but the first were born during the summer.

This suggested that the small snakes were attracted to the structure. To obtain information on how many snakes and which species were using the ant mound as a hibernaculum, a confinement cage was devised to surround the mound so that the occupants could be captured and recorded as they emerged from beneath the ground. The confinement trap consisted of a cone of hardware cloth (⅛ inch mesh) 3 feet in diameter at the base and 3 feet high. Six inches of the cone apex were cut off to facilitate free access of my hand to the interior to remove snakes. The base of the cone was reinforced with an inch-wide strip of sheet metal that was buried to a depth of 1 to 2 inches and packed solidly with dirt to prohibit animals from escaping. An outside fence, 2½ feet in height, was placed surrounding the cone trap. A small funnel entrance opened from this fence to the area between the fence and the cone. Snakes that approached or were returning to the mound and followed the circular fence would ultimately encounter the funnel opening. If an animal en-

tered, its only escape was through the 1 inch opening at the inside end of the funnel which was 2 inches above the ground level. With these traps most, if not all, vertebrate occupants of the ant mound were recorded when they came to the surface and remained there, and any trend for snakes to re-enter would be indicated.

The confinement trap was placed over the ant mound early in March of 1950 before the ground had begun to thaw. Prior to this on January 3, during an unusually warm spell, two ribbon snakes (born summer before) were observed sunning at this mound and were marked and released into the mound tunnels. The trap remained over the mound until mid-July to insure the capture of all the vertebrates present. The results of this trapping procedure are listed in Table I.

The first 10 snakes captured in the confinement trap were recorded and again released within the cone to test whether there was another exit from the mound. All of these were again taken from the trap, most of them within three days, but two, three weeks later. All other snakes taken from the cone trap were released three feet east of the mound. None returned to be captured in the funnel trap surrounding the cone trap, although five other adult snakes were captured there.

The period of emergence from hibernation was quite extended, from March 27 until May 30. Vetas (1951) indicates a spread of emergence from early April to late May for a den of striped racers (*Masticophis t. taeniatus*) and Great Basin rattlesnakes (*Crotalus viridis lutosus*) in Utah. Observations on activity near the ant mound also showed an extensive period of entrance into the hibernaculum.

All snakes, representing five species, were either young of the previous summer (1949), or juveniles, i.e., young from the summer of 1948. An adult striped chorus frog (*Pseudacris nigrita triseriata*) and a small Jefferson's salamander (*Ambystoma jeffersonianum*) were also recorded. In the fall of 1950, after the trap had been removed, snakes were recorded at the mound on two separate occasions. On October 25, one common garter snake, two ribbon snakes, and one Butler's garter snake were sunning, and on November 1, one common garter snake and one Dekay's snake were observed. All had been born during this summer.

The ant mound was excavated on February 25, 1951. The digging was done very slowly with a trowel so that accurate data on position, depth, cloacal temperatures, and other features that might prove to be pertinent to hibernation in poikilotherms could be gathered. Digging was stopped at 30 inches because of darkness.

TABLE I. *Dates of emergence of snakes and amphibians from an ant mound near Dixboro, Washtenaw County, Michigan, 1950*

Species	Date of emergence													Species total
	March		April						May					
	27	30	3	7	15	16	16	28	2	3	10	16	24	31	
Common garter snake	6	4	7		2(1J)	4(1J)	3(1J)	1	7(1J)	4	2			1	41(4J)
Ribbon snake	1		2		1(J)										4(1J)
Butler's garter snake	3	1	5			2	2	1	3		2	1	5		25
Common water snake									2						2
Smooth green snake									1(J)						2(1J)
Dekay's snake			1												1
Jefferson's salamander			1												1
Chorus frog				1											1

J = juvenile snakes born summer of 1948, all other snakes born summer of 1949.

TABLE II. *Species of snakes and amphibians recorded at various depths in an excavated ant mound, Washtenaw Co., Mich., Feb. 25, 1951*

Species	Depth (inches)													Specie totals
	0–5*	6–7	8–9	10–11	12–13	14–15	16–17**	18–19	20–21	22–23	24–25	26–27	28–29	
Common garter snake		1(3°) J		2(5.8°)	4(3.4°) (1J)	4(6.7°)	1(1.5°)	4	6	2		1(J)	1	26
Ribbon snake	3(1D)		1(5.6°)		3(5.8°)	3(5.4°)			1					11
Butler's garter snake						1			7	3	2	2		15
Common water snake	1(D)			1(D)					2					4
Smooth green snake									1(4°) J					1
DeKay's snake			2(9.5°)											2
Red-bellied snake						2(10°)								2
Unidentified snake					1(D)									1
Jefferson's salamander				1				1						5
Chorus frog		1	2	1		3			3					9
American toad		1 T							2					1

J = juveniles born summer 1949 (all other snakes born summer 1950).
D = dead.
T = transformed summer 1950.
* = soil temperature 1° C.
** = soil temperature 2° C.
Numbers in parentheses are individual or average cloacal temperatures (Centigrade).

The tunnels continued to go deeper and it is possible that there were more occupants present. The hibernaculum tunnels were interconnecting and while only 8 openings were found before excavating the mound, 18 separate tunnels were counted at a depth of 6 inches. The tunnels spread out underground so that the diameter of the area at one foot of depth was about three feet. This exceeded the original dimension of the mound above ground by one foot. The lower tunnels in this clay soil were very damp and many of the lowest ones reached were flooded. It is very possible that the snakes in the lowest tunnels were submerged in water.

Of the 77 vertebrates taken from the mound, 62 were snakes representing 7 species, and 15 were amphibians of 3 species. The numbers, depth at which found, and cloacal temperatures (taken of only a few) are shown in Table II. Many slugs, earthworms, ants, crickets, beetles and sow bugs were taken from all depths of the tunnels.

The six-inch portion of the mound that protruded above the ground level had a dead ribbon snake (born summer of 1951), which appeared to have been frozen. Otherwise, the first living records were for two ribbon snakes two inches below the ground level, eight inches beneath the upper surface of the mound. The common water snake (*Natrix s. sipedon*) that was found at 10 inches was in a state of decay and the cause of death could not be determined. Most specimens were very sluggish, but did have the ability to move and flick their tongues when prodded.

There is a tendency for one species to average higher or lower than another. With respect to the ribbon snake and Butler's garter snake at the ant mound, this difference was noticed in two ways. First, in the spring of 1945, the ribbon snakes were the first to appear near the mound and they also appeared here later in the fall than Butler's garter snakes. In 1950, all of the ribbon snakes had emerged by April 15, but Butler's garter snakes continued to emerge until May 24. Second, this may be correlated with the respective positions of these two species in the excavated mound. The ribbon snakes averaged higher in the tunnels than Butler's garter snakes. Because of the shape of many of these tunnels, it would not be possible for many of the individuals in the lowest tunnels to emerge until those above them had moved out. The difference between the times of emergence

from hibernation, at least for those two species, may be related to their depth in the hibernaculum. Further work should be done to see if this is correlated with temperature tolerance. The amphibians were generally scattered at all levels.

The body positions in which the hibernating snakes were found varied considerably. These variations may have been the result in some instances of the shape, size, and direction of the tunnels. Of those animals stretched out full length in the tunnels, some had their head at the upper end and others at the lower end of the tunnels. Some individuals were doubled once, with the head either higher, level with, or lower than the rest of the body. About one-half of the snakes were slightly coiled, the others were fully extended. The striped chorus frogs were in level tunnels, while the Jefferson's salamanders were headed both up and down. These vertebrates were not coiled together in masses but were scattered throughout the tunnels. Two individuals were frequently together in a small tunnel, in various combinations of the species represented.

The cloacal temperatures of the snakes show that the temperature is generally above that of the surrounding environment and that deeper snakes have a slightly higher cloacal temperature than those nearer the surface. That some of these snakes were above the frost line and had survived at this level seems certain, but a few nearer the surface may have been killed by severe cold. Bailey (1949) has shown that *Thamnophis radix* may survive sub-freezing temperatures up to 28 days. I have recorded many cloacal temperatures of snakes during cold weather which were higher than those of their environment. Lueth (1941) observed that at low temperatures, the body temperature of a snake is above that of its environment.

Of the snakes taken from the ant mound, eight had previously been captured and marked. Four had been marked late in the fall of 1950. These included a common garter snake, marked at the mound, two Butler's garter snakes, one captured 50 feet from the mound and the other 5 feet from the mound, and a Dekay's snake marked at the mound. All had been born the preceding summer. The other four had been trapped by the confinement trap as they emerged from the ant mound in the spring of 1950. Three were common garter snakes, and the other was a smooth green snake. All had been born during the summer of 1949, and were the only snakes of this age group taken from the mound. All others were one year younger. One of the common garter snakes was recorded on October 31, 1950, 176 feet east of the hibernaculum.

The ant mound was used as a hibernation site by young snakes and small amphibians from 1948 to 1950 and probably had been used for some time before this and would have continued to be used had it not been excavated. The den studies of Woodbury (1951) and his students were followed for 10 seasons. They had many returns of individuals year after year. In my study, by the following fall most small snakes at the ant mound had grown to a size that would generally prohibit them from entering the small tunnels, and this was presumably the reason that more of them did not return year after year.

Meadow Vole Tunnel

On March 28, 1949, a few days after the first snakes emerged from hibernation, 15 small snakes, all born the previous summer, were captured in a few minutes' time within a small area of approximately 100 square feet (800 feet east of the ant mound). They represented 4 species of which 11 were ribbon snakes, two common garter snakes, one Butler's garter snake and one common water snake. All had presumably been hibernating near by and were sunning themelves. A hibernaculum was found later in this area.

On January 2, 1950, a warm winter day (8.5° C.), while looking for sunning snakes on this same area, the head of a

small ribbon snake was noticed disappearing down a small hole about one inch in diameter. As the entrance of this tunnel was opened, the tail of a snake was seen 6 inches down. Between this depth and the end of the deepest tunnel at 15 inches, 16 snakes of 6 species and 3 amphibians of 2 species were removed. They were as follows: 3 adult common garter snakes and one adult Dekay's snake; two common garter snakes, five ribbon snakes, one Butler's garter snake, three common water snakes, and one smooth green snake, all young of the summer of 1949. The amphibians removed were two Jefferson's salamanders and one striped chorus frog.

About one-third of the snakes were coiled together at the eight-inch level where the tunnel widened to form a small chamber. This group contained the frog and salamanders as well as young and adult snakes. The rest of the snakes were scattered singly and stretched out in small tunnels down to the lowest depth observed. This underground chamber appeared to be that of a meadow vole (*Microtus pennsylvanicus*) and had two runways just beneath the surface, one running 10 feet west and the other 3 feet north. The snakes were located in such a manner that it would not have been possible for the lower snakes to emerge until those above had moved out. All the snakes were marked, returned to the excavated cavity, and covered to simulate as closely as possible the conditions under which they had been found. When this cavity was opened again late in the spring, only the decayed remains of a single garter snake were present. One of the marked snakes was captured about a year later showing that it, at least, had survived.

Crayfish Burrow

When snakes were observed in the spring and the late fall near the openings of tunnels, these points were recorded for future investigation. One such hole, a crayfish burrow, which had a large garter snake near it early in the spring of 1950, was checked on February 24, 1951. The crayfish burrow was located at the base of a six-foot hawthorn bush on the flat area between the south-facing grass-sumac hill and the marsh. The ground was still frozen in many places and this particular hole was plugged with ice. The removal of the first piece of sod around the hole revealed a snake in a small cavity partially filled with water. The water level was three inches below the surface of the ground. The snake started to move farther back into the cavity, which extended a short distance around the roots of the bush. The technique followed was to dig out and follow down the hole with a trowel, reaching ahead of the digging as far as possible to capture any animals present. Table III gives the results of this procedure.

Table III. *Results of excavation of flooded crayfish burrow used as snake hibernaculum, Washtenaw Co., Mich., Feb. 24, 1951*

Depth (inches)	Species	Cloacal temperature (° C.)
3	Common garter snake	4.2
16	Common garter snake	3.4
21	Common garter snake	5.0
22	Common water snake	7.0
23	Burrowing crayfish	
27	Common garter snake	6.8

The tunnel had a number of bends, and these, plus the very cold water (2° C. when first opened) and the hard clay soil made the digging difficult. Since the water in the burrow would flow higher when an arm was thrust down, a side trench was constructed to drain it off. This trench soon filled up, indicating that the water level was just beneath the ground surface. The cloacal temperatures were taken as soon as the snakes were removed from the hole. Digging was stopped at 35 inches because this was as far down as the shoulder and arm could reach. The diameter of the burrow varied from 1½ to 2 inches. At least the lower four snakes must have been totally submerged in the water and the deepest snake recorded was below the burrowing crayfish (*Cambarus diogenes*), the probable builder of this hibernaculum. Of the five snakes removed,

all were adults, 3 males and 2 females, four of which had been marked previously during the warm seasons.

On January 3, 1950, an adult common garter snake was observed sunning, and while this individual was being captured two adult common water snakes were found about one foot away. By searching closely in the grass at this area an opening to a burrow was revealed. This tunnel was completely flooded. While taking notes and watching this hole, the front part of a snake's head appeared above the water. As it emerged and became aware of my presence, it withdrew into the burrow leaving only its nose out of the water. On reaching to capture it, it went deeper beyond the reach of my fingers. A few minutes later, when I returned, a very wet and muddy common garter snake was next to this entrance, presumably the same snake that had emerged during my short absence. I later placed a small confinement cage over this opening, and on April 4, 1950 a small adult common water snake had emerged from the burrow through a small celluloid trap door placed over the entrance and was attempting to escape. Excavation of this burrow in February 1951 proved it to be that of a crayfish, but no snakes were found down to a depth of three feet. The tunnel was also flooded at this time.

Approximately four feet from the burrow just mentioned were two similarly flooded holes. As I was about to turn my attention from these, a movement was noticed in one of them, and a few seconds later a striped chorus frog emerged from beneath the water. One of these frogs had also been found near the hole previously mentioned.

The findings presented indicate very strongly that many snakes hibernate completely submerged in water in underground tunnels. It seems that this should be possible provided the water is very cold. Turtles and frogs regularly hibernate at the bottoms of pools and small lakes. The soil where the hibernacula studied were located consisted of a hard clay with very little organic material. Pope (1937) mentions a common water snake being taken from beneath five inches of water in a spring in western New York state. The water temperature was about 60° F.

Predation

Evidence indicating that snakes hibernating in crayfish burrows may be preyed upon by the crustaceans was gathered on a number of occasions. On January 2, 1950 while passing the opening of a crayfish burrow, the tail of a garter snake was noticed down in the tunnel. When this snake was removed, another snake could be felt deeper in the hole. Both snakes were adult *Thamnophis* and had most of the head and fore-part of the body destroyed as if they had been fed upon. Whether these snakes had been killed by the crayfish is not certain, but their presence in the burrow probably indicates that they were eaten by the crayfish.

On February 24, 1951 the remains of two snakes were found next to the entrance of a crayfish burrow. The remains of one was only a skeleton, but the other showed evidence of having been fed upon. The rotting remnants of a Dekay's snake were found at the ice-plugged entrance of another such burrow on March 3, 1951. On December 12, 1949, a dead adult common garter snake was found half-way out of a crayfish burrow, but it showed no evidence of having been fed upon.

Under warm conditions an adult snake would not be ready prey for a crayfish, but in the torpid state of hibernation they would be easy prey.

On November 2, 1948, an adult common water snake was located in what probably was its hibernaculum. It was uncovered about one inch beneath the leaf litter at the base of a bush thicket near the top of a wooded hill, 15 feet above water level and 40 feet from the marsh. It was coiled beneath the damp leaves and was very sluggish. There was lose dirt beneath the leaves and numerous tunnels led into the base of the bushes. Adult common water snakes in this area were

seldom seen outside the marsh except in the late fall. One fall an adult male was observed coiled on a large rock on a hillside in the woods about 30 feet from the marsh, and another was captured crawling through dense grass down a ravine about 40 feet from the marsh. This activity would indicate that some individuals of this species may move away from the marsh to higher ground to hibernate.

Discussion

The places used as hibernacula are structures that have been made by animals other than the reptiles and amphibians using them for winter dens. This suggests that there may be a close relationship between the abundance of these poikilotherms and the available hibernation sites.

The dens observed were near the marsh at ground level close to the water table and not up on the hillside in the better drained soils. This may be related to the necessity of moisture for successful hibernation, because low temperatures quickly dehydrate. It is well known that frogs and turtles hibernate under water, but this is not generally known to be true of snakes. The evidence gathered here suggests that at least the common water snake and the common garter snake may hibernate completely submerged. It has often been suggested that snakes recorded as active in winter and others found active early in the spring have been "flooded out" of hibernation. It seems more likely that the warm rains penetrate down to hibernating forms and this warmth stimulates them to become active.

It is not uncommon to find a number of species or a large number of individual snakes using the same hibernaculum (Woodbury 1951; Gloyd 1944; Pope 1937), but seven species of snakes associated with salamanders, frogs, and a toad is an unusual association. Criddle (1937) records taking 8 *Thamnophis radix*, 101 *Storeria occipito-maculata*, and 148 *Opheodrys v. vernalis* from an ant hill in Manitoba. The amphibians recorded from the Michigan regions are the normal food of the snakes during warmer seasons, and an association at this time would certainly not be of any benefit to the amphibians. They are evidently attracted by similar requirements for hibernation sites during the fall after feeding has ceased and move out from hibernation before the snakes are actively feeding in the spring.

Summary

A number of hibernacula including an ant mound, crayfish burrows, and a vole tunnel were studied in Washtenaw County, Michigan. The following species of snakes and amphibians were found associated on excavation of these structures: *Thamnophis s. sirtalis, Thamnophis s. sauritus, Thamnophis butleri, Natrix s. sipedon, Opheodrys v. vernalis, Storeria dekayi, Storeria occipitomaculata, Ambystoma jeffersonianum, Pseudacris nigrita triseriata,* and *Bufo a. americanus*. Evidence gathered from the excavations indicates that snakes may hibernate submerged completely beneath water. Cloacal temperatures of snakes were higher than those of the surrounding environments. Some variation of preferred hibernating depth, perhaps related to time of emergence, was indicated. Burrowing crayfish may prey upon snakes hibernating in their burrows. A confinement trap was used in studying emergence from the ant mound.

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THE RATE OF ORGANIC MATTER ACCUMULATION ON THE SEDGE MAT ZONES OF BOGS IN THE ITASCA STATE PARK REGION OF MINNESOTA

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INTRODUCTION

In any discussion of the rate of net accumulation of organic matter, a working knowledge of the various factors which influence the rates of deposition and decomposition is indispensable. It is obvious even to the most superficial observer that at least part of the organic matter deposited each year upon the earth's crust must decay, otherwise the earth would long ago have been completely covered by a layer of plant and animal remains many feet thick. A survey of the world literature on this subject reveals that deposition and decomposition of organic remains rarely proceed at equal rates. In humid equatorial and tropical regions annual organic deposition is very great but decomposition is also very rapid so that no net accumulation results. In arctic regions, at the other extreme, the frost table may rise during the winter following the brief growing period when the organic layer was laid down, never to thaw again; under these circumstances annual deposition and accumulation are almost identical and decomposition may be negligible except along stream banks and on slopes strongly inclined toward the equator. In mid-latitudes, organic deposition is intermediate and the rate of decomposition varies especially with kinds of plants, and local temperature, drainage, and aeration. On humid upland surfaces, the situation may closely approach that of the moist tropics; in poorly drained depressions decomposition may be very slow because of inhibiting influences of high water table, poor aeration, high acidity, and low temperature.

Thus we see that the rate of organic matter accumulation under any vegetation type depends not only upon the amount of organic remains deposited but also upon the rate at which these deposits are acted upon by decomposing agents. In other words, accumulation is the net result of deposition minus decomposition. If decomposition is equal to or exceeds deposition, no accumulation occurs. If deposition exceeds decomposition, accumulation will occur, the amount depending upon the difference in the two rates.

Studies on the rate of organic matter accumulation

Attempts have been made to measure the amount of organic matter accumulation under various kinds of native vegetation, but it is probable that such measurements also include the preceding growing season's deposition before decomposition has taken place. Hence these estimates cannot be considered as true organic matter accumulation (the net result of deposition minus decomposition). Sims (1930) reported an accumulation of three to four tons of air-dry litter per acre in the pine-oak forests of the southern Appalachians. Bodman and Kittredge (1937), working in various forested regions of northern California, found the average thickness of litter to vary from 1.2 cm. to 4.9 cm. Billings (1938) found that organic matter in the surface soils of abandoned fields in the Piedmont of North Carolina increased steadily during shortleaf pine (*P. echinata* Mill.) succession from 0.85 per cent in a

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recently abandoned field to 2.94 per cent in a 110 year old stand. Larson and Whitman (1942), while studying undisturbed grasslands of a mesa in South Dakota, found a surface mulch averaging ¼ to ½ inch in thickness. Auten (1945) estimated an accumulation of 7,000 pounds per acre under sassafras, 10,000 pounds per acre under black locust, and 20,000 pounds per acre under pines in reforested stands, 21 to 35 years old, on formerly cultivated fields in Illinois, Indiana, and Ohio. Campbell (1946) measured seasonal variations in the rate of accumulation of liter on burned and unburned forest range of Louisiana. On unburned grass plots, accumulation of litter decreased from 3,235 pounds per acre in February to 1,310 pounds in September due to grazing and rapid decomposition during high summer temperatures. In oak woods, accumulation decreased from 688 pounds per acre in March to 518 pounds per acre in October. Under pines, accumulation decreased from 2,142 pounds per acre in March to 860 pounds per acre in October. Dyksterhuis and Schmutz (1947) reported an average accumulation of 7,464 pounds per acre of organic matter on a Texas prairie.

In addition to the above studies, considerable work has been done on the rate of peat accumulation in bogs. From the outset, it should be recognized that the rate of peat accumulation is not a uniform process but rather depends upon a multiplicity of factors, each of which influences the amount and rate of accumulation. According to Bjorling and Gissing (1907), a high relative humidity and a mean annual temperature ranging a few degrees below or above 7° C favor the most rapid accumulation, although this is probably too great a simplification of the many climatic variations in which peat occurs throughout the world.

The kind and amount of vegetation which forms the raw material for peat formation is likewise very important. In the Lake States region of the United States, peat deposits which accumulate in ponds or lakes generally go through the following successional stages according to Soper (1919):

(1) Stonewort-waterweed stage (*Chara-Philotria* associes),
(2) Pondweed-water lily stage (*Potamogeton-Nymphaea* associes),
(3) Rush-wild rice stage (*Scirpus-Zizania* associes),
(4) Bog-meadow stage (*Carex* associes),
(5) Sphagnum-bog heath stage (*Andromeda-Ledum* associes),
(6) Tamarack-spruce stage (*Larix-Picea* associes).

The rate of deposition of organic matter is considerably slower in the first three pond stages than in the latter three bog stages. Accumulation of organic matter reaches its greatest rate in the sphagnum-bog heath stage. In fact, sphagnum itself is considered the most valuable of all peat-forming plants (Soper 1919).

Gradual compaction is one of several factors that make it extremely difficult to ascertain the rate of peat formation. Others are drought, fire, and wave action. A period of drought permits the entrance of oxygen and aerobic microorganisms, thus resulting in rapid decomposition of the surface organic matter and a lowering of the surface of the bog due to decreased volume. The occurrence of fire in many bogs in past years has resulted in the alternate burning and rebuilding of the peat deposits, the extent of which is almost impossible to ascertain accurately. Wave action is most pronounced on peat bogs bordering large lakes. In such instances the peat and the vegetation producing it has undoubtedly been eroded away and rebuilt many times in the past due to fluctuations in lake level and wave action (Soper 1919).

Estimates as to the rate of peat formation are numerous and vary from 2 years per foot in certain areas of Germany to 1,650 years per foot in the Great Lakes region of the United States (Sears and Janson 1933). However in practically all

of these studies, the species composition of the peat has been sadly neglected. It has been shown previously that the kind of vegetation is very important in determining the rate of accumulation. Undoubtedly many of the large discrepancies in these estimates are based, at least in part, upon the failure to recognize and analyze this factor. In general it may be said that the more extreme estimates are based upon insufficiently supported evidence. Disregarding these extremes, estimates have a tendency to center around values of 100 to 800 years per foot for average well-consolidated peat.

To the writer's knowledge, the only study which has dealt with the surface accumulation of organic matter in bogs and subsequent peat formation is that by Sears and Janson (1933). Unfortunately the methods and procedures followed are only briefly summarized, and the data, while apparently showing good correlation, are based on too many asumptions to be considered as representing an accurate picture of the rate of peat formation. Data are presented from two bogs, one in northern Ohio and one in Michigan. The study of the Ohio bog revealed a series of laminations of the peat 18 to 24 inches below the surface. This peat, on the basis of pollen analysis, was found to belong to the oak-pine period which correlates with a 24 foot depth near Wooster, Ohio. It was assigned an age of 6,000 to 8,000 years. The shallow depth of the peat was due to extensive humification, and to fire and surface erosion. The laminations of this peat were due to alternate layers of algal jelly and sedge leaves. Interpreting these layers as being annual in character, an average rate of peat accumulation was calculated as 300 years per foot.

Attempts to find similar laminations in the Michigan bog were unsuccessful, but it was possible to separate the most recent layers down to a depth of eight or ten inches. Measurement of these layers showed a rapid decrease from a mean thickness of 2.1 inches at the surface to a mean thickness of less than 0.25 inch in the eighth to tenth layers. Data for greater depths were secured from isolated spruce and tamarack trees in the bog. The age of each was ascertained by means of an increment borer. Pits were then dug below each tree and a careful search conducted for needles as far down as they could be found. (This procedure would imply that the increment borings were taken before the pit was dug and hence taken at or above the surface level of the bog. If such was the case, then the age determinations for each of these trees is too low, and error would increase with the age of the trees as the germination level and annual growth cylinders produced at the stem base in the first few years became more and more deeply buried.) A total of 15 trees was studied in this manner, their ages ranging from 17 to 70 years. The depth of the needles ranged from 8 inches under the 17 year old tree to 14 inches under the 70 year old tree. In contrast to the rapid compaction of the upper eight or ten layers, subsequent compaction appeared to be very slow. Presenting these data on a graph, an approximate exponential curve representing the rate of peat compaction was drawn. The original data collected from the Ohio peat samples, believed to be 6,000 to 8,000 years old and at an equivalent depth of 24 feet, were then plotted on this graph and showed a close correlation with the curve.

In conclusion the authors state, ". . . there appears to be a period of maximum compression during the first 15 to 20 years, and after that much slower compression. Comparing the measurements, such as they are, for the first 70 years with those from peat certainly between 6,000 and 8,000 years old, it does not appear far wrong to speak of a mean rate of peat accumulation of between 20 and 30 years to the inch for the past several thousand years, in the Great Lakes area."

Studies of this kind but involving more accurate procedures and including data regarding the plants and parts involved are very much needed to provide basic information on the amount of surface accumula-

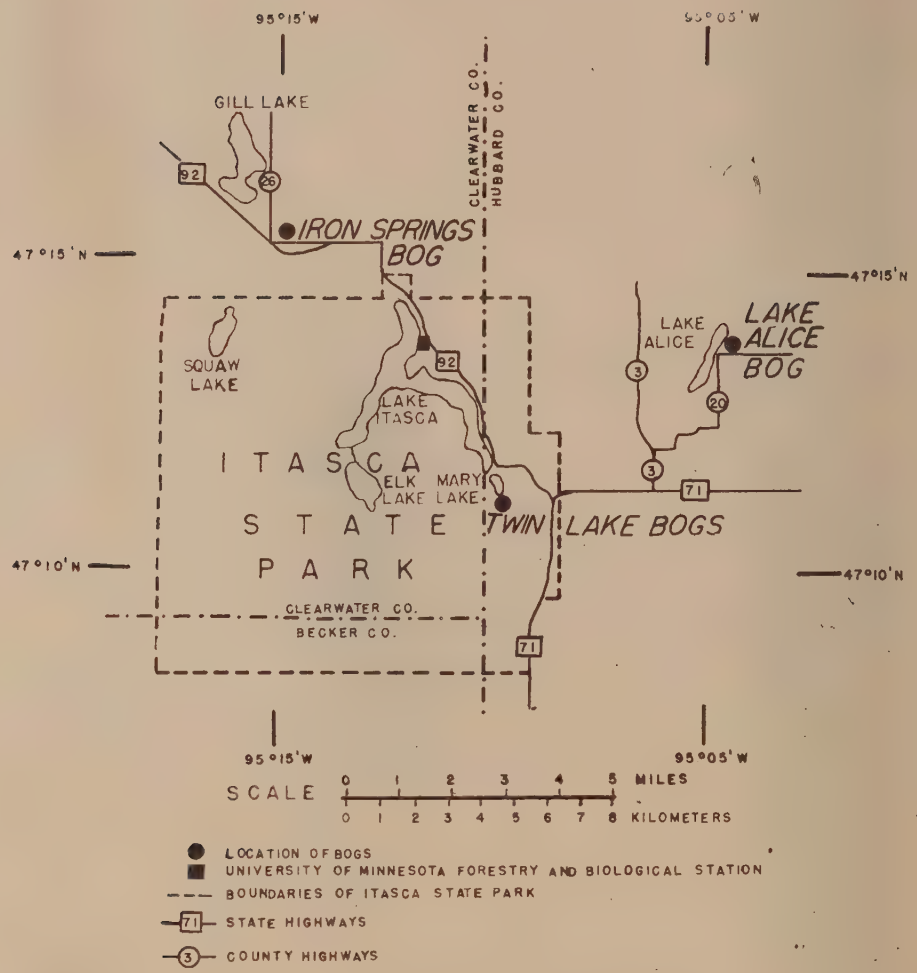

FIG. 1. Map of the Itasca State Park region showing location of the bogs in this study.

tion of organic matter from which the amount of compaction and decomposition which have taken place in the underlying peat may be calculated. It was with this thought in mind that the present study was undertaken. Since the study reported in this paper is limited to seven stations in an area of approximately 100 square miles in north-central Minnesota, the results cannot be applied to a wide region, but it is hoped that the methods outlined will be useful to workers in other areas.

METHODS AND PROCEDURES

Field work on this problem was carried on during the summer of 1951. The selection of bogs to be studied was largely influenced by the descriptive article of Conway (1949) on the bogs of central Minnesota, and by the excellent facilities provided by the Forestry and Biological Station of the University of Minnesota located at Itasca State Park, where some of the bogs described by Conway are available, still relatively undisturbed by

man. After study of aerial photographs and actual observation of various bogs in this region, the following bogs were selected for study: Lake Alice bog, Iron Springs bog, and four of the six Twin Lakes bogs. A general map (Fig. 1) of the Itasca State Park region shows the location of these bogs. The average elevation of this area is approximately 1,400 feet above sea level.

The sedge mat zones of these six bogs were selected for study, since it is only in these zones that a relatively even surface is presented. The moss-heath and bog forest zones, with their extensive areas of sphagnum hummocks, were avoided because of the difficult task of selecting a reference surface from which to measure the accumulation of organic matter. In addition, any measurements conducted in these areas would be, for the most part, merely measurements of the growth rate of sphagnum, since the hummocks of the moss surround practically every tree seedling. Tree seedlings, as will be seen, are the means used in the present study of measuring the rate of accumulation.

Identification of all Angiosperm species in this study was confirmed by consulting Gray's manual (Fernald 1950) and by comparison with herbarium specimens at the Forestry and Biological Station. The names given in the text for these species are those of Fernald (1950). The mosses listed in the text were identified by Dr. Richard I. Evans of the University of Wisconsin, all names and authorities being taken from Grout (1928).

Method of measuring rate of accumulation

Seedlings of tamarack (*Larix laricina*) were used in this study as an index of the rate of peat accumulation, since in most

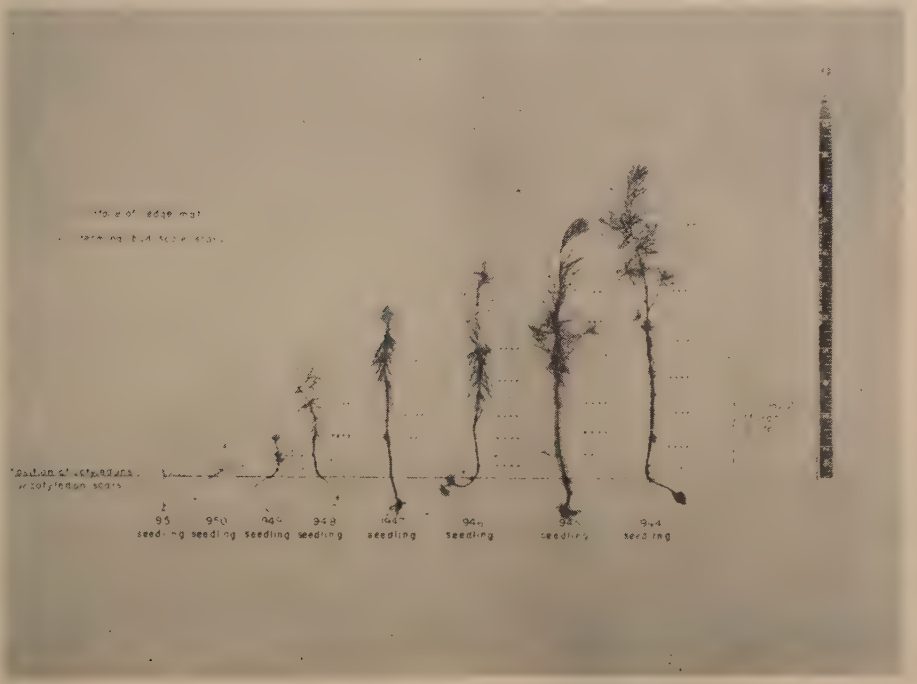

FIG. 2. A series of tamarack seedlings illustrating the vertical accumulation of organic matter over a period of seven years. Scale is in inches.

cases, they were relatively plentiful on the sedge mat zones and the age and depth at which they germinated were easy to ascertain. At each station, seedlings of various sizes and ages were gathered with stem and root intact (Fig. 2), each seedling stem being carefully notched with a knife at the level of the surface of the sedge mat at the time of gathering. Special care was taken to collect as many of the current year's crop of seedlings as possible, since measurement of all older seedlings was based upon the position of the cotyledons on the current year seedlings. Large seedlings or young trees were, for the most part, avoided in order to eliminate the factor of settling which was thought might result from the weight of older, heavier trees.

In each case, the place of insertion of the cotyledons on the stem or the ring of cotyledon scars was used as a reference point on the seedling stem, the position of insertion of the cotyledon bases in relation to the surface of the sedge mat at germination being ascertained by examination of the current year's seedlings as will be shown later. With each seedling being notched at the surface level of the sedge mat, it was thus possible to measure the vertical distance from the surface to the cotyledon bases or the cotyledon scars. Outline drawings (life-size) were made on coordinate paper of each freshly collected seedling with special care taken to maintain the same vertical orientation of the upper part of the seedling as when gathered in the field. Many of the seedlings examined showed a pronounced curvature of the subsurface portions of the stem and main root, thus making it imperative that true vertical orientation of the seedling be maintained in order to measure accurately the vertical extent of organic matter accumulation. On each outline drawing of a seedling, the position of the base of the cotyledons or ring of cotyledon scars and the surface level of the sedge mat as indicated by the notch made at the time of gathering were marked by pencil. Using these two marks as reference points, the vertical distance between them was then measured and recorded. In those cases where the underground stem and root were decidedly curved, a horizontal line was drawn through the cotyledon scars and a vertical line erected upon this to pass through the bog surface level, thus ensuring an accurate vertical measurement of the amount of accumulation.

The age of each seedling was then ascertained by counting, and recording beside the seedling sketch, the number of terminal bud scale scars (excluding the cotyledonary ring). In those cases where the bud scale scars were indistinct, the age of the seedling was ascertained by making a series of cross-sections of the shoot-root axis near where the seedling collet (junction of shoot and root) was thought to be; the largest number of rings, minus one, counted with the aid of a $2\frac{1}{2} \times$ lens, was recorded as the number of years that peat had been accumulating about the seedling.

We have no way of knowing exactly what the relation of the newly expanded cotyledons was in relation to the peat surface in the older seedlings at the time when vertical growth of the hypocotyl ceased the first year. However, the cotyledons must have been at, slightly above, or at least not far below the general peat surface in order to have received the light requisite for survival of the seedling. The subsequent vertical growth rate of the seedling must continually have exceeded or at least equalled the vertical yearly accumulation of the peat. Seedlings with vertical growth slower than the peat must necessarily have been eliminated. The position of the seed upon germination must have been a sufficient distance below the peat surface to obtain the continuous moisture necessary for germination and early seedling growth.

In order to find out the relation of cotyledon level to peat surfaces of varying densities, several *Larix* germinates with completed height growth for the year were collected at each station, the number of germinates collected depending upon their availability at each station. The vertical

distance of the cotyledon ring above or below the general peat surface was measured for each and the average calculated for each station. This average figure, which was taken as the standard, was then subtracted from or added to the vertical measurements of each of the older seedlings at each respective station (it being assumed that conditions on the average at the time of germination of the older seedlings were the same as in 1951). For example, if the average position of the cotyledon ring at a certain station was 0.2 inch (0.41 cm) below the surface on current year seedlings, this figure (0.2 inch) would be subtracted from all measurements of older seedlings from this station. Similarly, if the average position was 0.2 inch above the surface, 0.2 inch would be added to each measurement of older seedlings.

After this correction factor was applied to each seedling the measurements were then totaled and averaged. Yearly averages on the vertical rate of organic matter accumulation were obtained both for each age class represented and for the composite average for all age classes at each station.

It will be noted that there is a decided majority of seedlings in the 1948 and 1945 age-classes. This predominance is probably due to very good seed years in 1947 and 1944, resulting in many seedlings the year following the shedding of the seeds. According to Duncan (1951), there was a bumper crop of seed produced in 1947 at Itasca State Park. The seed crops in 1948 and 1949 were either just fair or poor. These observations were confirmed by unpublished data from the Lake States Forest Experiment Station which also indicated that 1945 and 1946 were poor to fair crop years in this general area. Unfortunately no data were available for 1944, but it is likely that this was also a very good seed crop year.

Method of collecting and analyzing peat volume samples

In addition to merely measuring the rate of depth accumulation, it was considered

FIG. 3. Peat sampler at the left with a resulting peat volume sample at the right.

that measurements of the kinds and amounts of organic material that contribute to this accumulation would be highly desirable. Therefore, natural volume samples of surface peat were collected at the various stations by means of a tin can, both ends of which were removed, leaving the stiffening flange intact at the top but providing a toothed cutting edge along the bottom edge by means of a tinsnips (Fig. 3). The dimensions of the can were 3 × 4¼ inches (7.6 × 10.7 cm) thus giving a volume sample of approximately 30 cubic inches (485 cc.). The area where the peat sample was to be collected was first cleared of all growing vegetation down to the surface level. The can was then twisted into the sedge mat until the top edge was flush with the surface. A pit was then dug around the can until the bottom edge of the can was accessible. By means of a knife, the peat was cut flush with the bottom edge of the can (tips of the teeth). The sample was then carefully removed from the can and wrapped in waxed paper. In this manner, a number of equal-volume samples was collected at each station. Special care was taken to collect the peat samples in the exact locality in which the seedlings were gathered to ensure accurate correlation of the results of the sample analysis with the rate of accumulation as measured by the seedlings themselves. Later, while each collection was still moist, they were carefully divided, as described later, into species segregates and these dried in an oven at 103–

105° C so that the portion which each kind of plant contributed to the peat accumulation could be ascertained.

Only three samples could be analyzed at the Forestry and Biological Station, due to time limitations, and the rest of the samples were sprinkled with naphthalene crystals (about one tablespoon per sample) soon after collection and wrapped in three or four layers of waxed paper. These were brought back to the botany laboratory at the University of Minnesota for analysis. The naphthalene crystals were added to the samples to reduce bacterial and fungal decomposition of the organic matter. In spite of this precaution, a slight amount of fungal growth was evident on a few of the samples, and in four cases living earthworms were found 12 to 16 weeks later. However, this fungal growth was so slight that it undoubtedly did not affect the final weights to any significant extent. Since the naphthalene crystals readily sublimed at oven temperatures, they did not affect the final oven-dry weights of the various components.

Analysis of all samples was completed 18 weeks after the time of collection. In spite of this long period of storage at room temperature for many of the samples, it is doubtful whether any significant respiration of the peat had occurred. The 3 samples from Lake Alice Station A which were analyzed at the Forestry and Biological Station showed approximately the same values for the different major components as those samples from the same station analyzed 16 weeks later. The average total weight of the 3 samples (19.29 gms.) was somewhat higher than the average total weight (18.24 gms.) of the 7 samples analyzed later, but this cannot be considered significant because of the small number of samples involved. Storage of the samples at near freezing temperatures would undoubtedly be more advisable than room temperature, since respiration and decomposition, if any, would thus be reduced to a minimum.

The use of waxed paper for wrapping the peat samples proved to be far from satisfactory. The high water content of the samples and the action of microorganisms quickly deteriorated the inner layers of the waxed paper, thus making it extremely difficult to separate the paper from the sample. It is suggested that the use of plastic refrigerator bags or aluminum foil would prove much more satisfactory for storage of peat samples.

The method of analysis was as follows: the peat sample, after being unwrapped, was dissected into small pieces to facilitate handling. Each piece was placed in a large beaker of water and squeezed like a sponge with the fingers until all of the decomposed matter was washed free. Material of the different plant species which made up the sample was separated and placed in separate beakers. After all pieces were washed and separated, the solution containing the decomposed material was passed over a wire screen basket with openings slightly less than $\frac{1}{16}$ inch (1.6 mm). The residue on the screen, consisting of portions of the different plants which were broken off during the squeezing operation, was thoroughly washed free of any clinging decomposed material and then separated into species components as before. All of the wash water was gathered in a single beaker and allowed to stand for 24 hours until the excess supernatant water could be poured off. This beaker containing the decomposed matter and those containing the different plant remains were placed in a drying oven set at 103–105° C for a period of 24 hours. At the end of this period, the oven-dry weight of each component was ascertained to the nearest hundredth of a gram. The weights of the various fractions were then totaled and the percentage of the total calculated for each component. In addition, the volume-weight (W/V) for each sample was ascertained by dividing the total oven-dry weight in grams of the various fractions of the sample by the volume of the sampling can (485 cc).

It should be stated that the decomposed organic matter fraction for each sample

undoubtedly contained more than just organic matter. Atmospheric dust, silt and clay washed down from surrounding slopes, and mineral precipitates from the water surely must have contributed to some extent to the final weight of this fraction. The extent of the contribution of these inorganic materials was not determined due to time limitations but it is suggested that analyses should definitely separate these in future work.

Five peat volume samples were analyzed for each station with the exception of Lake Alice Station A where 10 samples were analyzed. Originally it was hoped that 10 samples might be analyzed for each station, but the process of separating the peat into its various components proved to be very time-consuming (approximately 3 hours per sample). Furthermore, percentages of the different components in the 5 samples at each station varied so little, that the extra time required for further analysis of more samples was not deemed profitable.

Certain general characteristics of the peat volume samples may be cited at this time. The uppermost half-inch or so of the sample usually consisted entirely of freshly deposited plant remains of various species with negligible decomposition having occurred. Beneath this layer and throughout the rest of the sample the sedge roots and rhizomes formed an extensive interwoven network. Most of the decomposed matter in the sample was found interspersed in this network as well as those plant remains which could resist rapid decomposition, such as twigs and woody rootstocks, tamarack needles, and other highly cutinized leaves.

Description and Data for Each Station

Twin Lakes Area

The Twin Lakes area is located within the boundaries of Itasca State Park just south of Mary Lake. It consists of a series of depressions each showing an excellent example of bog succession. Figure 4 shows the location of these depressions,

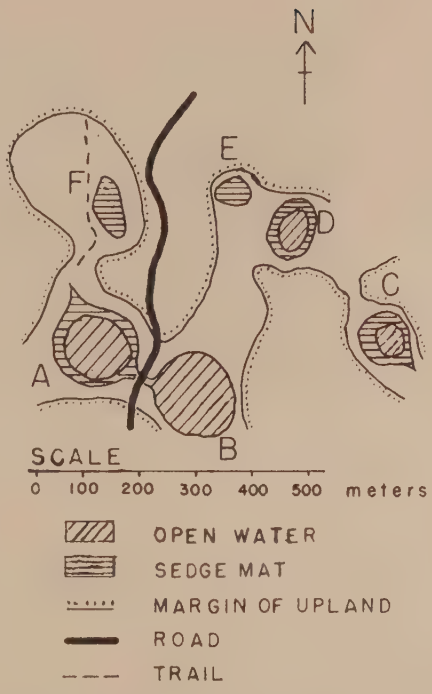

Fig. 4. Sketch-map of Twin Lakes area showing location of the various stations (after Conway 1949).

each of which is lettered according to Conway's (1949) description of the area. A and B, the so-called "Twin Lakes," showed signs of interference, such as the building of fences and cutting of trees, and were therefore not included in the study. The rest of the bogs were, however, relatively undisturbed and represented ideal locations for the collection of data.

The type of bog succession was essentially similar for each of these stations. The pioneer sedge mat, consisting mainly of *Carex lasiocarpa* var. *americana* was still invading the open water at C and D, while at E and F the completed sedge mat entirely covered the center of the bog. At each station *Larix laricina* directly invades the sedge mat without the usual intermediate stage of a moss-heath community. *Larix* is in turn followed by black spruce (*Picea mariana*), which in most cases formed an understory beneath the tamarack.

FIG. 5. General view of Twin Lakes Station C showing *Carex lasiocarpa* in the foreground as the most abundant sedge mat species with *Carex comosa* and *Typha latifolia* predominant along the water's edge.

Twin Lakes Station C.—Station C, the most inaccessible of the Twin Lake bogs, showed very well defined stages of bog succession. The sedge mat, still encroaching upon the open water, was predominantly composed of *Carex lasiocarpa*. Along the open water edge of the sedge mat, *Carex comosa* and *Typha latifolia* were predominant, apparently indicating that these two species are the active invaders of open water followed by *Carex lasiocarpa* once the sedge mat has become established (Fig. 5). A number of other Angiosperms were also present on the sedge mat, including *Menyanthes trifoliata* var. *minor* and *Salix* sp., but these were distinctly a minor element. Among the Bryophytes, *Drepanocladus aduncus* was observed to be by far the most abundant.

As in all of the Twin Lake bogs, the bog forest directly invades the sedge mat with tamarack observed to be the most active invader followed closely by black spruce. At the time of observation, there appeared to be very little encroachment on the sedge mat of the bog forest as indicated by the absence of seedlings along most of the bog forest margin. However, at the southeast corner of the sedge mat active invasion was definitely taking place. It was in this area that all of the seedlings and peat volume samples were collected. A total of twenty-seven 1951 seedlings were found and upon examination showed an average position of the cotyledons of 0.05 inch (0.13 cm) above the surface of the sedge mat. This correction factor was subsequently added to all measurements of older seedlings.

The results of these measurements are shown in Table I and indicate an average rate of organic matter accumulation of approximately 0.57 inch (1.45 cm) per year. Table II indicates the results of the peat volume sample analyses. *Carex lasiocarpa,* as might be expected, makes up the major portion of the samples, almost 70 per cent. The decomposed organic matter fraction is the second largest component, contributing almost 26 per cent. The average volume-weight was 0.045.

Twin Lakes Station D.—Station D was quite similar to C. *Carex lasiocarpa* again predominated on the sedge mat with *Carex comosa* and *Typha latifolia* generally confined to the wetter southern and western portions and along the open water edge of the sedge mat. The northern portion of the sedge mat was considerably firmer and drier than the rest, and it was only in this region that tamarack reproduction could be found. Invasion of the sedge mat by tamarack is undoubtedly proceeding at a very slow rate as is shown

TABLE I. *Rate of organic matter accumulation for each station*

Age class of seedlings	Twin Lakes C		Twin Lakes D		Twin Lakes E		Twin Lakes F		Lake Alice A		Lake Alice B		Iron Springs	
	Number of seedlings measured	Avg. acc. per year in inches	Number of seedlings measured	Avg. acc. per year in inches	Number of seedlings measured	Avg. acc. per year in inches	Number of seedlings measured	Avg. acc. per year in inches	Number of seedlings measured	Avg. acc. per year in inches	Number of seedlings measured	Avg. acc. per year in inches	Number of seedlings measured	Abg. acc. per year in inches
1950	1	0.45	—	—	—	—	1	0.34	—	—	—	—	—	—
1949	—	—	—	—	—	—	4	0.47	8	0.62	4	0.57	—	—
1948	21	0.61	2	0.67	—	—	36	0.52	125	0.60	66	0.61	67	0.68
1947	—	—	1	0.76	—	—	5	0.67	3	0.63	2	0.47	2	0.76
1946	4	0.57	—	—	—	—	2	0.37	5	0.49	2	0.40	3	0.73
1945	23	0.56	10	0.68	4	0.84	22	0.56	21	0.49	33	0.61	14	0.64
1944	—	—	—	—	—	—	—	—	2	0.61	1	0.80	—	—
1943	—	—	—	—	—	—	—	—	3	0.52	—	—	—	—
1942	—	—	—	—	—	—	—	—	2	0.50	—	—	—	—
1941	—	—	—	—	—	—	—	—	2	0.36	—	—	1	0.72
1940	—	—	—	—	—	—	—	—	2	0.32	—	—	—	—
1932	—	—	—	—	1	0.73	—	—	—	—	—	—	—	
	49	0.57*	13	0.68*	5	0.79*	70	0.54	173	0.55*	108	0.61*	87	0.67*

* Average based on the sum of depths of accumulation around all seedlings divided by the sum of the ages of all seedlings.

TABLE II. *Averages of analyses of peat volume samples on oven-dry basis for each station*

Species	Twin Lakes C		Twin Lakes D		Twin Lakes E		Twin Lakes F		Lake Alice A		Lake Alice B		Iron Springs	
	Weight in grams	Per cent	Weight in grams	Per cent	Weight in grams	Per cent	Weight in grams	Per cent	Weight in grams	Per cent	Weight in grams	Per cent	Weight in grams	Per cent
Carex lasiocarpa var. *americana*	14.98	69.20	15.78	73.16	6.60	70.73	12.64	45.34	12.57	67.76	11.61	70.00	12.48	52.58
Drepanocladus aduncus	0.37	1.73	1.17	5.41	1.34	14.37	0.70	2.53	—	—	—	—	—	—
Drepanocladus vernicosus	—	—	—	—	—	—	—	—	0.49	2.62	1.06	6.37	1.37	5.78
Dicranella squarrosa	—	—	—	—	—	—	—	—	0.57	3.05	—	—	—	—
Aulacomnium palustre	—	—	—	—	—	—	—	—	0.49	2.65	0.70	4.21	—	—
Climacium dendroides	—	—	—	—	—	—	—	—	0.11	0.60	—	—	—	—
Larix laricina	0.11	0.52	0.33	1.52	0.06	0.62	0.66	2.38	0.06	0.31	0.01	0.04	0.21	0.87
Menyanthes trifoliata var. *minor*	0.01	0.06	—	—	—	—	—	—	—	—	0.18	1.09	0.27	1.15
Salix sp.	—	—	—	—	0.01	0.09	—	—	0.04	0.20	0.02	0.11	—	—
Vaccinium oxycoccus	—	—	0.03	0.15	0.21	2.25	0.01	0.03	0.10	0.52	0.05	0.30	0.03	0.13
Mnium sp.	—	—	—	—	—	—	0.02	0.06	—	0.01	—	—	—	—
Betula pumila var. *glandulifera*	—	—	—	—	—	—	—	—	0.04	0.22	0.02	0.10	—	0.02
Andromeda glaucophylla	—	—	—	—	—	—	—	—	0.01	0.03	—	—	—	—
Viola pallens	—	—	—	—	—	—	—	—	0.01	0.03	—	—	—	—
Drosera rotundifolia	—	—	—	—	—	—	—	—	—	0.02	—	0.01	—	—
Unidentified material	0.60	2.75	0.05	0.22	0.24	2.61	0.37	1.32	0.32	1.75	0.24	1.47	0.31	1.29
Decomposed organic matter	5.57	25.73	4.22	19.54	0.87	9.33	13.47	48.34	3.75	20.23	2.70	16.31	9.06	38.19
Totals	21.64	100.00	21.58	100.00	9.33	100.00	27.87	100.00	18.56	100.00	16.59	100.01	23.73	100.01
Volume-weight	0.045	—	0.045	—	0.020	—	0.057	—	0.038	—	0.034	—	0.049	—

by the low number of seedlings occurring on the sedge mat.

A total of thirteen 1951 seedlings were found and showed an average position of the cotyledons of 0.10 inch (0.25 cm) above the surface of the sedge mat. This figure was subsequently added to measurements of the older seedlings.

The average rate of organic matter accumulation as indicated by the measurements of these seedlings was 0.68 inch (1.73 cm) per year (Table I). *Carex lasiocarpa* again made up the major portion of the peat samples, contributing about 73 per cent, while the decomposed organic matter fraction (19½%) and *Drepanocladus aduncus* (5½%) comprised the other major components (Table II). The average volume-weight was 0.045.

Twin Lakes Station E.—Station E, the smallest of the Twin Lake bogs, had its center completely covered by a sedge mat at the time of this study. According to local observations, open water existed as recently as 1941 in the center of the bog. The rather loose and unconsolidated nature of the surface peat in the center of the sedge mat would also tend to confirm a recent completion of the mat. *Carex lasiocarpa* was again the dominant species on the sedge mat, although *Carex comosa* was present to a greater extent than at other stations due to very moist conditions. The water table at Station E was very high, extending to within an inch or so of the surface. Because of this fact, seedling reproduction was almost nonexistent. In fact, no 1951 seedlings were found, and only five older seedlings could be collected. Since no 1951 seedlings were avaliable, no correction factor could be applied to the measurements of these older seedlings. The average rate of organic matter accumulation as indicated by these older seedlings was almost 0.79 inch (2.01 cm) per year, which is somewhat higher than at other stations (Table I). However, it is interesting to note the measurement of the 1932 seedling. This tamarack had been repeatedly browsed so that in spite of being 19 years old it was only about 2 feet tall and light in weight, hence eliminating the possibility of settling. The rate of accumulation of organic matter as shown by this seedling, 0.73 inch (1.85 cm), would seem to indicate very little consolidation or compression of the uppermost 13 inches of organic matter. Such a general inference, however, is extremely hazardous, since it is based upon only one seedling with no correction factor applied. The unusually high water table which undoubtedly hindered normal decomposition and compression is probably responsible for the high value recorded for vertical rate of accumulation.

The loose, fluffy, uncompressed nature of the surface organic matter is shown by the average volume-weight of the peat samples (0.020), which is only about half that at other stations (Table II). Because of the absence of oxygen induced by the high water table, decomposition of the organic matter was proceeding much slower than normal. This is indicated by the low percentage (about 9½%) of the decomposed organic matter fraction. *Carex lasiocarpa* (almost 71%) and *Drepanocladus aduncus* (almost 14½%) were the two major components of the peat samples.

Twin Lakes Station F.—The completed sedge mat at Station F (Fig. 6) was considerably firmer and better developed and is undoubtedly older than the sedge mat at Station E. The northern portion of the mat was drier and firmer than the southern portion, with *Carex lasiocarpa* dominating the former and *Carex rostrata* var. *utriculata* the latter. Due to this moisture factor, seedling reproduction was limited to the northern portion (Fig. 7), and hence the data obtained are representative only of this area. Tamarack reproduction is undoubtedly favored by a relatively dry, firm-textured sedge mat, such as at this station, since more seedlings were found here than at any of the other Twin Lake stations. A total of thirty-one 1951 seedlings were

FIG. 6. General view of Twin Lakes Station F looking across the completed sedge mat in the foreground.

found, the relative position of the cotyledons being 0.04 inch (0.10 cm) beneath the surface of the sedge mat. This correction factor was subtracted from all measurements of older seedlings. Table I shows the rate of organic matter accumulation at Station F as indicated by the measurements of these seedlings. The average rate of accumulation, 0.54 inch (1.37 cm) per year is slightly less than at any of the other Twin Lake stations.

The high percentage (almost 48½%) of the decomposed organic matter fraction in the peat volume samples for Station F, as shown in Table II, and the slower rate of accumulation as compared with Stations C and D are explained as probably resulting from a more rapid rate of decomposition of the organic matter. *Carex lasiocarpa* (almost 45½%) and the decomposed organic matter fraction were the two major components of the peat samples. The very high volume-weight (0.057) is undoubtedly due to the weight of the decomposed organic matter fraction.

Lake Alice Bog

Lake Alice bog, located approximately 6 miles east of the Forestry and Biologi-

FIG. 7. Young tamarack growing along the northern edge of the sedge mat at Twin Lakes Station F.

cal Station, is perhaps the best example of bog succession in the entire area. (The bog itself is not related to Lake Alice, being located one mile east of it, but this lake is the nearest named topographic feature). It is undoubtedly shallower than any of the Twin Lake bog lakes as is shown by the large proportion of floating-leaf hydrophytes which extend over the entire surface of the water. The sedge mat zone is again dominated by *Carex lasiocarpa,* although the extent of this zone is very narrow around most of the open water (Fig. 8) except along the northern edge of the bog where it forms an extensive meadow. In contrast to the Twin Lake bogs, a well-developed moss-heath zone is present which is actively colonizing the sedge mat everywhere except along the northern edge of the bog. *Betula pumila* var. *glandulifera* and *Andromeda glaucophylla* are the conspicuous members of the moss-heath zone along with a variety of mosses quite different from those found on the sedge mat. *Drepanocladus vernicosus* is predominant on the sedge mat, while *Sphagnum* sp., *Aulacomnium palustre,* and *Dicranella squarrosa* are the most important mosses on the moss-heath zone. The bog forest, dominated by *Larix laricina* in the younger stage and *Picea mariana* in the older, forms a wide zone behind the moss-heath zone. Seedling reproduction of *Larix* is very abundant in the moss-heath community, apparently indicating a rapid invasion of this zone by the bog forest. Because of this abundance of reproduction, a large number of seedlings were available for measurement as indicated in Table I.

Due to the variation in extent of the sedge mat, it was deemed advisable to make collections both in the area of active colonization by the moss-heath zone (Station A) and in the area where the sedge mat is relatively stable (Station B).

Lake Alice Station A.—Station A was located along the southwest edge of Lake Alice bog where the moss-heath zone actually forms an admixture with the sedge mat zone due to its rapid invasion of this zone. Collection of tamarack seedlings and peat volume samples was confined to the patches of sedge mat still existing, but even so a number of moss-heath species were already present as is shown in Table II. A total of forty-nine 1951 seedlings were collected and showed an average position of the cotyledons of 0.30 inch (0.76 cm) above the surface of the sedge mat. This correction factor was added to all measurements of older seedlings.

Table I indicates the rate of accumulation of organic matter at Lake Alice Sta-

FIG. 8. Lake Alice Station A showing the relatively narrow extent of the sedge mat zone.

tion A. The average rate of accumulation, considering all of the seedlings measured, was approximately 0.55 inch (1.40 cm) per year. Those seedlings in the 1942, 1941, and 1940 age class were actually young trees about four to five feet high. Whether the average rate of accumulation as shown by these young trees, 0.50 inch (1.26 cm), 0.36 inch (0.91 cm), and 0.32 inch (0.82 cm), respectively, is sufficient to show compaction of the lowermost peat layers is highly problematical. It was observed that the amount of vegetative growth beneath these trees was considerably less than out in the open, undoubtedly due to the shading effect of the trees themselves. The lower rate of accumulation could thus be accounted for by the smaller amount of organic residue deposited on the surface.

Table II shows the great variety of plant remains which made up the peat volume samples. *Carex lasiocarpa* contributed almost 68 per cent of the ovendry weight of the samples, the decomposed organic matter fraction about 20 per cent, and the mosses, *Dicranella squarrosa, Aulacomnium palustre, Drepanocladus vernicosus,* and *Climacium dendroides,* about 9 per cent. The average volume weight of the samples was 0.038.

Lake Alice Station B.—Station B was located along the north-west edge of the Lake Alice bog where the sedge mat was 50 to 75 yards wide. Tamarack reproduction in this area was not as widespread as at Station A, but about 100 seedlings were still available for measurement. A total of twenty-nine 1951 seedlings were measured and showed an average position of the cotyledons of 0.55 inch (1.76 cm) above the surface of the sedge mat. This correction factor was added to all measurements of older seedlings.

Table I indicates a slightly higher average rate of accumulation of organic matter than at Station A, the rate being approximately 0.61 inch (1.54 cm) per year. It should be noted that the average for the 1945 and 1948 age-classes, the two most abundant, are almost exactly the same (0.613 and 0.610 inch, respectively) indicating very little change, if any, in the yearly rate of accumulation up to that point.

Table II indicates the results of the peat volume sample analyses. *Carex lasiocarpa* formed 70 per cent of the ovendry weight of the samples, the decomposed organic matter fraction about 16 per cent, and the mosses, *Drepanocladus vernicosus* and *Aulacomnium palustre,* about 10½ per cent. The average volume-weight of the samples (0.034) was almost the same as at Station A (0.038).

Iron Springs

The Iron Springs bog is located about one mile north of Itasca State Park, just north of Highway 92. It differs from the other bogs in this study in that it is formed about an active spring rather than being formed around a lake or pond. The continuous year-round flow of water from this spring has formed flow lines across much of the surrounding lowlands, thus creating a favorable environment for a bog community. At the time of this study, these flow lines were completely covered by vegetation, but their paths could be easily followed by observing the characteristic reddish precipitate which was deposited from the drainage waters of the spring.

As might be expected in this sort of a bog, there were no well-defined vegetation zones, although the general successional pattern was similar to other bogs. The sedge mat zone existed as patches of vegetation interspersed in areas dominated by *Betula pumila* or young *Larix.* These patches probably represent the last remains of a former more extensive sedge mat. In this connection, it was surprising to note the very lush growth of *Carex lasiocarpa,* although this may be due to the high mineral content, especially in iron compounds, of the drainage waters. A

more or less poorly developed moss-heath zone could be distinguished dominated by *Betula pumila,* although the characteristic *Andromeda glaucophylla* of the Lake Alice bog was entirely absent. The bog forest, consisting in the younger stages of *Larix laricina* and in the older of *Picea mariana,* formed a very extensive zone surrounding the study area. Active colonization of the moss-heath and sedge-mat zones by *Larix* was occurring throughout most of the area, apparently at a very rapid rate as was inferred from the large number of young trees and seedlings observed.

A total of twenty 1951 seedlings were measured and showed an average position of the cotyledons of 0.10 inch (0.25 cm) above the surface. This correction factor was added to all measurements of older seedlings.

The average rate of accumulation of organic matter as shown by the measurement of tamarack seedlings collected in the sedge mat areas is indicated in Table I. The average rate of accumulation per year, 0.67 inch (1.70 cm), is slightly higher than at most of the other bogs. This increase may be due to the very dense growth of *Carex lasiocarpa* as indicated previously.

The results of the peat sample analyses, as shown in Table II, indicate an unusually high percentage (38%) of the decomposed organic fraction. This undoubtedly was due to the addition of mineral compounds and silt and clay particles carried by the drainage waters. Each of the peat samples had a characteristic reddish color indicating that deposition of iron compounds had definitely occurred. *Carex lasiocarpa* made up 52½ per cent of the remaining total and *Drepanocladus vernicosus* almost 6 per cent. The contribution of other species was almost negligible. The high percentage of the decomposed fraction is reflected in the volume-weight (0.048) which is higher than all other stations except Twin Lakes Station F.

TABLE III. *Rate of organic matter accumulation for the Itasca State Park region*

Age class of seedlings	Number of seedlings measured	Average accumulation per year in inches
1950	2	0.395
1949	16	0.57
1948	317	0.61
1947	13	0.65
1946	16	0.53
1945	123	0.58
1944	3	0.68
1943	3	0.52
1942	2	0.50
1941	3	0.48
1940	2	0.32
	500	0.59(1.50 cm)*

* Average based on the sum of depths of accumulation around all seedlings divided by the sum of the ages of all seedlings.

ANALYSIS OF THE DATA

From the foregoing data, it is evident that the average yearly rate of organic matter accumulation at each of the stations is quite similar. Excluding Twin Lakes Station E, for which no correction factor was available, the rate varies from 0.54 inch (1.38 cm) at Twin Lakes Station F to 0.68 inch (1.73 cm) at Twin Lakes Station D. Since the rate of accumulation for each station shows such little variation, the data from all stations have been combined into a single table (Table III) which indicates the average rate of accumulation for each seedling age-class. (The data from Twin Lakes Station E have not been included in this table, since no correction factor was available.) The 1949, 1948, 1947, 1946, and 1945 age-classes, which comprise over 95 per cent of the seedlings measured and are therefore the most reliable, show remarkably little variation, 0.53 to 0.65 inch (1.34 to 1.65 cm), in the yearly rate of accumulation. Moreover, this similarity might even be extended through the 1944 and 1943 age-classes, although the small number of seedlings collected in these age-classes precludes any definite conclusion. Since the data obtained are based, for the most part, on the measurements of a great number of seedlings (317 in the 1948 age-class and 123 in the 1945 age-class) and should there-

fore be reliable, we may conclude that the average rate of accumulation of organic matter on the sedge mat zones of bogs in the Itasca State Park region is slightly more than a half-inch per year, and that this rate is fairly constant over a period of at least the first 6 to 8 years of accumulation. In no instance was there any positive indication that any compaction of these upper peat layers had occurred, although the occasional pronounced curvature of the subsurface portions of the stem and main root previously mentioned may be indicative of such compaction locally.

These results are in direct contrast to the findings of Sears and Janson (1933) which indicated a rapid decrease in the thickness of the uppermost peat layers to approximately ⅛ of the original thickness at the end of 8 or 10 years. At first glance, the data of Sears and Janson would seem to be more logical, since continued decomposition and compaction of the deposited organic remains would be expected to decrease the volume of these layers. However, this fails to account for the extensive growth of sedge roots and rhizomes throughout these upper peat layers. It must be remembered that the growth of sedge roots and rhizomes also contributes to the volume of the upper peat layers, in fact possibly to a much greater extent than the deposition of plant material which occurs upon the surface. Clipping studies would be needed to estimate separately the material contributed by aerial and non-aerial parts. The subsurface growth extends to an unknown depth, but living roots and rhizomes were observed at least an inch or two beneath the level of the bottom edge of the peat sampler.

One must realize that the measurements reported in the present study do not include the lowermost level of root and rhizome growth. It is possible that the subsurface growth with its buoyant lacunar tissue may be sufficient to raise appreciably the surface layers of the peat and the seedlings themselves. Since elevation of the surface layers would effectively lower the water table, increase aeration and decomposition, and thereby reduce accumulation, this process should be evaluated if possible in any further work of this sort. This could be accomplished if a continuous core sample were taken from the surface downward as far as necessary to include all the material produced by the sedges. Changes in buoyance with time could be ascertained by measuring the buoyancy of isolated whole cores collected along a transect from the lake margin to older portions of the sedge mat.

It is the writer's opinion that in the Itasca State Park region the yearly volume of growth of sedge rhizomes and roots in the uppermost 4 inches is approximately equal to the yearly decrease in volume of the deposited organic remains due to decomposition and compaction. This would account for the fairly constant rate of accumulation shown in this study for the top 4 inches. Beneath the depth of root and rhizome growth, decrease in the volume of the peat layers is undoubtedly occurring, but this was not confirmed in the present study.

The average oven-dry weight of the peat volume samples was 19.90 grams. This represents the average weight of a cylinder of surface peat with a diameter of 3 inches and a depth of 4¼ inches (the dimensions of the peat sampler). Assuming an average rate of accumulation of 0.6 inch per year, 14.11 per cent of the 19.90 grams would be added yearly. This is the equivalent of 2.8 grams being deposited yearly on an area of 7.07 square inches. Converting these values to a pounds-per-acre basis, we find that 5,477 pounds of organic matter per acre (1,005 kilograms per hectare) per year are deposited on the average in the uppermost 4 inches of the sedge mat zones of bogs in the Itasca Park region. Since some of the annual photosynthate is surely going into the roots and rhizomes that develop below the sampling depth, this figure of course does not represent the total deposition from the sedge plants but only the deposition included in the sampled portion of the profile.

Harmer (1941) states that the dry

weight of mineral soils varies from 75 to 100 pounds per cubic foot, the weight of muck from 15 to 30 pounds per cubic foot, and the weight of peat from 6 to 20 pounds per cubic foot. Converting these figures to a volume-weight basis, the following values are obtained:

Mineral soil	1.20–1.60
Muck	0.24–0.48
Peat	0.09–0.32

These values represent the average volume-weights of surface soils and thus can be compared with the average volume-weight of the surface peat samples collected from the various stations in this study. By averaging all of the volume-weights for the various samples collected, a composite volume-weight value of 0.041 was computed. Since these samples included the surface litter and undoubtedly contained much more undecomposed material than an agricultural peat soil, and since the living roots and rhizomes contain a high proportion of lacunar tissue, they should therefore be expected to have a lower volume-weight.

Since the volume of a surface inch of peat is considerably reduced by compaction and further decomposition beneath the surface, the volume-weight should increase proportionally according to depth. Unfortunately no determinations of this sort were conducted, but a comparison of the volume-weights of peat samples taken at the surface and at different depths in a bog might be helpful in estimating the amount of compaction and decomposition that has occurred.

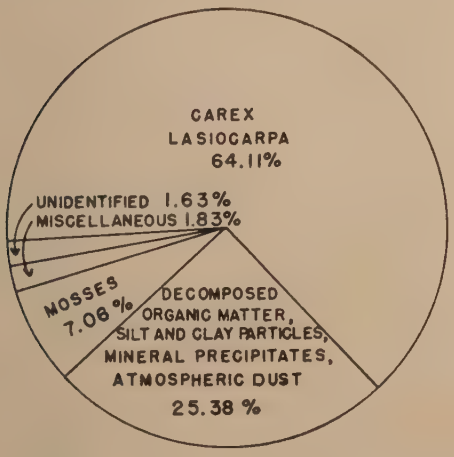

Fig. 9. Diagram representing the average composition of the surface four inches of peat on the sedge mat zone including the decomposed organic matter fraction.

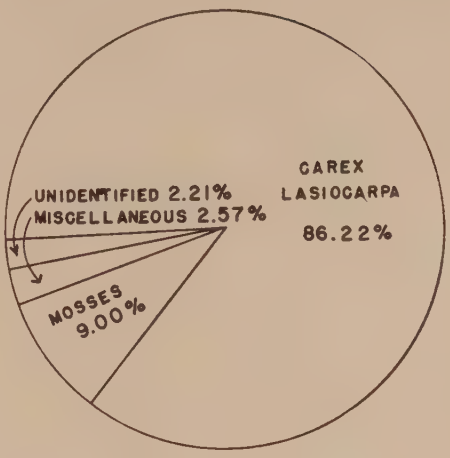

Fig. 10. Diagram representing the average composition of the undecomposed plant remains in the surface four inches of peat on the sedge mat zone.

The average composition of the peat volume samples for all stations is shown in Figure 9. *Carex lasiocarpa* comprises the largest fraction, 64.11 per cent, while the decomposed organic matter fraction, made up of decomposed organic matter, slit and clay particles, mineral precipitates, and atmospheric dust, is next with 25.38 per cent. These two fractions make up almost 90 per cent of the surface peat samples. The remaining 10 per cent is composed of mosses (7.06%), miscellaneous species (1.83%), and unidentified material (1.63%).

Since the amount of the decomposed organic matter fraction varied so greatly from station to station (9.33 to 48.34%), the average percentages of the other fractions for each station and the composite average percentages for all stations, excluding the decomposed fraction, were cal-

culated (Fig. 10). The average composition of the undecomposed plant remains consists of 86.22 per cent *Carex lasiocarpa,* 9.00 per cent mosses, 2.57 per cent miscellaneous species, and 2.21 per cent unidentified material.

Summary

Organic matter accumulation is the net result of deposition minus decomposition. Various estimates on the amount of organic matter accumulation under native vegetation in different areas are given.

Six bogs in the vicinity of Itasca State Park were selected for the study of the rate of organic matter accumulation on the sedge mat zones: four of the six Twin Lake bogs, Lake Alice bog, and Iron Springs bog.

Seedlings of tamarack ranging in age from germinates of the current season to 11 years were used as an index of the rate of peat accumulation. The depth of accumulation around each seedling was measured from the surface level down to the cotyledons or cotyledon scars, and the depth of peat divided by the seedling age to obtain the annual accumulation rate. The position of the cotyledons in relation to the surface at germination was ascertained by examination of current year seedlings.

Measurements of the kinds and amounts of organic material that contributed to the accumulation of surface peat were ascertained by collecting surface peat samples at each station, separating each sample into the various species components, and weighing each fraction on an oven-dry basis. In addition, the volume-weight of each sample was calculated.

A brief description and data on the rate of organic matter accumulation and analyses of the surface peat samples are presented for each station.

Since the calculated rates of accumulation at each of the stations are quite similar, the data from all stations are combined into a single table. From this we may conclude that the average rate of organic matter accumulation in the top 4 inches of the sedge mat zones of bogs in the Itasca State Park region is slightly more than a half-inch per year (equivalent to about 24 years per foot). Apparently this rate is fairly constant during the first 6 to 8 years of accumulation.

Assuming an average rate of accumulation of 0.6 inch per year, a total of 5,477 pounds of organic matter per acre (1,005 kilograms per hectare) would be deposited annually on the sedge mat zone in the uppermost 4 inches.

The average composition of the surface peat samples including the decomposed organic matter fraction consists of 64.11 per cent *Carex lasiocarpa,* 25.38 per cent decomposed organic matter and inorganic material, 7.06 per cent mosses, 1.83 per cent miscellaneous species, and 1.63 per cent unidentified material. The average composition of the samples excluding the decomposed organic matter fraction consists of 86.22 per cent *Carex lasiocarpa,* 9.00 per cent mosses, 2.57 per cent miscellaneous species, and 2.21 per cent unidentified material.

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SOME FEEDING HABITS OF MOOSE IN YELLOWSTONE PARK

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INTRODUCTION

Moose, most majestic of all deer, command attention at all times and in all places. It is not unusual in Yellowstone Park to see over one hundred people per hour stop along the highway during the height of the tourist season to observe this animal. Moose are considered one of the prime attractions there.

Because of over-crowding of many species in a limited area and because of the obligation the Park Service has to the public, problems of wildlife management are particularly acute there. A complete monographic study of the moose with all of the intricate interrelationships is needed, but such a study would require years to complete.

Considerable interest has been shown in the moose of the region since Shiras (1913) made the initial study of the Yellowstone moose (*Alces americana shirasi* Nelson). Murie (1934) studied the moose of Isle Royale from a more strictly ecological approach and stressed the feeding habits. This paper is a portion of a study made on the feeding behavior of the moose of Yellowstone Park. Field studies include June 20 to September 7, 1947; June 4 to September 10, 1948; May 30 to September 10, 1949.

Yellowstone Park is located principally in the northwest corner of Wyoming. Except for some irregularities of boundary lines at the extreme northwest and northeast corners, the park extends into Montana 3.1 miles on the north and 2.05 miles into Montana and Idaho on the west. Willow Park and the adjacent Swan Lake Flat comprise the principal areas covered in this paper. These areas lie in a general north-south direction paralleling the main park highway about midway between Mammoth Hot Springs and Norris Geyser Basin.

METHODS OF STUDY

Direct observations were used almost exclusively to determine the food and feeding habits of the moose. Binoculars (7 × 35 mm.) were used in the field observations. Representatives of species of plants that were eaten by the moose were collected and mounted according to accepted herbarium methods and submitted for identification to specialists in the various groups.

In all cases where the time element enters, such as rate of movement while feeding, time spent in feeding, etc., the time was determined by watch. Distances covered in feeding are estimates only. Accuracy of estimates was checked twice by measuring with a steel tape and was found to be as great as the study required.

PLANTS EATEN

Although moose are primarily browsing animals, in no sense are they restricted to browsing. In this study twenty-three species of plants were found to be eaten. From a total of 1,497 observations it was found that two species of willow constitute approximately 75 per cent of the diet, while aquatic plants total a little over 17 per cent, both based on frequency of utilization; on the same basis grasses, grass-like plants, and forbs make up only 7.9 per cent of the total. On the basis of time spent in feeding on each type, willows constituted 88.5 per cent of the diet, aquatic plants 9.3, grasses, grass-like plants and forbs 2.2 per cent.

Schultz (1942) lists a total of seventy-one species of plants that were eaten by moose on the area involved in that study,

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and the list is admittedly incomplete. The area covered by the Montana study was several hundred times larger than the area used in the present one and involved three minor, but distinct, watersheds. Murie (1934) found a much greater utilization of trees and shrubs on Isle Royale than was found by either the present study or the Montana Survey. The reason for this is apparently the presence of a greater variety of species in a mixed hardwood and coniferous habitat than in the almost completely coniferous Yellowstone and Montana areas. Thus it appears that moose, while restricted in food preference to a certain degree, do have a wide range of selectivity. The greater the variety of species making up the plant cover of a particular locality, the greater is the number of species eaten by the moose.

Feeding on *Salix Geyeriana* is approximately three times more frequent than on *S. Wolfii*. Of 1,115 observations of moose feeding on willows, *S. Geyeriana* accounts for 73.1 per cent in contrast to 26.9 percent for *S. Wolfii*. Table I shows the percentage of observations for both willows figured on the basis of all species of plants eaten; out of a total of 1,497 feeding observations, 54.5 per cent were made of moose feeding on *S. Geyeriana* and 20.0 per cent on *S. Wolfii*.

The reasons for the difference in degree of browsing on the two species are not clear, but certain hypotheses may be advanced. Van Dersal (1938) lists these

TABLE I. *Distribution, abundance, number of observations, and percentages of the total of observations of utilization of plants eaten by moose*

Species	Occurrence	No. observations of utilization by moose	Per cent of total observations	Per cent total feeding time
Shrubs				
Salix Geyeriana	A—W	815	54.5	88.5
S. Wolfii	A—W	300	20.0	
Aquatic plants			17.5	9.3
Heteranthera dubia	P—Sc	78		
Myriophyllum sp.	M—Sc	68		
Potamogeton alpinus	R—TSc	4		
P. pectinatus	M—Sc	52		
Utricularia vulgaris	M—Sc	57		
Chara sp.	R—TSc	2		
Grasses			5.4	1.6
Agrostis hiemalis	S—Sc	6		
Agropyron sp.	S—TSc	18		
Deschampsia caespitosa	R—TSc	3		
Glyceria pauciflora	R—SmC	5		
Bromus ciliatus	S—TSc	3		
Elymus glaucus	S—TSc	3		
Melica bulbosa	R—TSc	3		
Phleum alpinum	M—Sc	4		
Poa sp.	M—Sc	37		
Forbs			0.9	0.5
Fragaria americana	R—TSc	1		
Heracleum lanatum	M—TSc	11		
Potentilla sp.	S—TSc	2		
Miscellaneous			1.6	0.1
Carex sp.	A—W	23		
Equisetum hiemale	R—TSc	1		
Luzula Wahlenbergii	R—SmC	1		

Scale used in above table: A—abundant; P—plentiful; M—moderate; S—scarce; R—rare; W—wide-spread; Sc—Scattered; TSc—thinly scattered; SmC—single small clump.

willows as being equally palatable for domestic stock and there is no apparent reason why they should not be equally so for wild animals. De Nio (1938), in discussing food and feeding habits of both deer and elk, makes no distinction between different species of willows with reference to palatability. Young (1938) says that all forms of willows are equally palatable. The term "palatability" is defined by the U. S. Forest Service as that percentage of the readily accessibly herbage of a species that is eaten when the range is properly utilized.

The fact that *S. Geyeriana* is tall enough in many places to hide the moose while feeding may account for part of the difference in frequency of utilization. *S. Wolfii* is rarely more than three feet tall and can scarcely hide an adult moose even when lying down. Moose may tend to avoid browsing on *S. Wolfii* because it is so low that it may be less easily browsed than taller shrubs. On this study area it was noted that elk browsed more on *S. Wolfii* than on *S. Geyeriana,* but this was largely due, I think to the fact that most of the *S. Wolfii* was found on the west side of the area and, therefore, farther from the highway. The elk are much more wary than the moose in this locality and only rarely were found feeding within three hundred yards of the road. The fact that elk tend to be more of a grazing animal than moose may explain, in part, why they feed more frequently on *S. Wolfii* than do moose.

Grasses constitute a minor part of the moose's diet. Only 5.4 per cent of the feeding records refer to grasses. *Poa* sp., being the most abundant and widespread of the grasses on the area, was observed to be eaten thirty-seven times. Wheat grass, *Agropyron* sp., was utilized eighteen times. Although this grass is scarce and thinly scattered it was eaten much more frequently than other grasses that are more abundant. While the data are too few to say that there is a preference for *Agropyron* sp., it appears that there may be. The other seven species of grasses constitute less than 2 per cent of the total number of feeding records.

Grass-like plants, of which *Carex* sp. constitutes all but two of the records in this group, furnish only 1.6 per cent of the feeding records.

Only three species of forbs were observed to be utilized. They make up less than 1 per cent of the total. Almost certainly others were taken by the moose, but were not observed. No seasonal variation in the diet was noted during the period of study.

Underwater Feeding

In this area aquatic plants constitute a minor part of the moose's diet. Very little of the total feeding time is spent in the old beaver canals and streams of the area. Two factors operate to relegate aquatic feeding to a secondary position. The amount of aquatic vegetation that is available to the moose as compared to the amount of willow browse is very small, and the soft bottoms of the sluggish streams and beaver canals make feeding there difficult. It appears as if aquatic plants serve only as a condiment to the staple food.

Eight different species of aquatic plants known to be eaten by moose are found on the study area. The yellow water lily, *Nymphaea polysepala,* which is normally considered a staple part of the diet elsewhere, was not seen to be eaten at any time. *Chara* sp., a plant heavily encrusted with calcium salts and therefore not considered to be very palatable, was seen to be eaten on only two occasions. *Spirogyra* sp., was not seen to be eaten by the moose on this area during the period of study. All three of these species are rare and are found in small, isolated patches. The yellow water lily was found in only two places with very few plants in each patch. Late in the summer the water dried up where these plants grew, and the leaves died down to the underground stem. I believe they were not

eaten simply because of the much greater availability of other species.

Heteranthera dubia was preferred above all others. In one instance a cow was seen to come from the woods and go directly to a patch growing in the shallow water of Obsidian Creek and feed on it for forty minutes. In getting to this place she ignored other aquatic plants which were easily available.

The water in the streams and canals was relatively shallow. In most places the depth ranged between six and twelve inches, except in a few places in Obsidian Creek where it was as much as six feet. Moose are capable of completely submerging themselves and feeding for as long as a minute without coming up to breathe. On this area, however, the water in which the moose fed was shallow enough so that it was largely a matter of simple grazing in the water. In eighty-six instances of moose feeding on submerged aquatic vegetation, the average length of time that the head was submerged was 10.3 seconds with a range of two to twenty-five seconds. The interval between submersions ranged from one to nineteen seconds, with an average of 4.6 seconds when feeding was continuous.

Mineral Diet

There are two small places in the study area where both moose and deer were seen to come to eat the soil. Numerous tracks indicated that elk also frequented them.

Often the moose would stand in Obsidian Creek and eat the soil of the bank. In one place about four feet long the bank is undermined about a foot. The bank here is wet due to seepage from a higher level. On one occasion a moose was seen to take a mouthful from underneath the overhang. Presumably the undermining was done by repeated eating of the soil by moose and elk.

On the opposite side of the stream and about thirty feet from the edge of the bank there is an area about thirty feet in diameter that is bare of vegetation, quite dry, and well trampled. It is rather high in the center, about two feet higher than the outer edge. I think possibly there may have been a beaver house on the spot in times past when beavers were more common in the area. This spot is also utilized as a source of minerals by moose, elk, and deer.

Samples of soil were taken from both places and qualitative analyses run on them. From the data contained in Table II it appears that the chlorides and sulfates of sodium and calcium were the minerals sought by the moose. It is questionable whether the iron was sought.

The moose were never seen at the licks during the day because they are within twenty-five yards of one of the main parking areas on the highway and there were cars parked there almost continuously during the day. Moose were observed at the licks as early as 7 P.M. and as late as 10:30 P.M.

The length of time the moose spent at the licks was always short, varying from several minutes to as long as half an hour. Both bulls and cows frequented the licks. No more than three were ever seen there at any one time, and that only once. Frequently there were two, but generally only one.

Table II. *Qualitative analysis of soil samples obtained from mineral licks*

Sample	Ca	Na	Cl	SO_4	Mg	K	PO_4	Fe
Moist bank of creek	Sl.	Sl.	Sl.	Sl.	Neg.	Neg.	Neg.	Neg.
Dry soil 30 ft. back from bank	Mod.	Mod.	Mod.	Mod.	Neg.	Neg.	Neg.	Faint

Scale: Neg., negative; Faint; Sl., slight; Mod., moderate.

TABLE III. *Frequency and percentage of types of browsing on willows*

How browsed	*S. Geyeriana*	*S. Wolfii*	Both species
No. twigs nipped	435	518	953
Per cent nipped	38.6	41.3	39.9
No. twigs stripped	80	99	179
Per cent stripped	7.0	7.7	7.5
No. twigs nipped and stripped	612	639	1,251
Per cent nipped and stripped	54.4	50.8	52.6
Total no. twigs examined	1,127	1,256	2,383

MANNER OF FEEDING

The moose is not a dainty browser like the deer; neither is it a coarse browser like the elk, when the elk is forced to browse. The browsing of moose can be divided into three categories, nipping, stripping, and a combination of these. In the process of nipping, the ends of the twigs are grasped between the lower incisors and premaxillaries of the upper jaw and broken off sharply by an upward or forward motion of the muzzle. The length of twig removed in this manner is relatively short, only two to four inches of the leafy end. The number of twigs taken in a single mouthful is variable, depending on the density of twigs on the central shoot. It is necessarily limited, perhaps being half a dozen twigs at the most. The lack of upper incisors precludes the possibility of cutting off large twigs by this means. The largest twig known to have been nipped by moose was three-sixteenths of an inch in diameter.

In stripping, the upper lip and tongue are used to gather a mouthful very much in the same manner as a horse. With an upward twist of the head the twigs are, in effect, pulled through the mouth, thus stripping them of leaves and small lateral shoots. The length of shoots stripped of leaves is also variable. The majority of twigs are stripped of their leaves for a length of four to twelve inches.

In feeding on willows very often the moose will strip off some leaves from the proximal portion of the twig and nip off the terminal bud as the twig is pulled through the mouth. The effect of removal of the lateral leaves and the terminal bud has a decidedly different effect on the response of the willow to browse injury as will be shown later.

Adult moose of this area have no difficulty in grazing on grass and sedge, but calves, because of their long front legs and relatively short neck, find it is necessary to kneel to graze.

In order to determine what part of the moose's feeding on willows consisted of nipping the ends of the shoot, stripping the leaves, and both, counts were made in six different places immediately after adult moose had fed there. Only twigs that were freshly browsed were counted so as to eliminate those browsed by elk. Table III shows that in browsing, over 50 per cent of a total of 2,383 twigs are both nipped and stripped in the process. When a shoot is stripped, quite obviously the terminal bud would stand a good chance of being removed. Approximately 40 per cent of the moose's feeding is done by nipping the ends of the twigs with no injury to the remaining lateral buds, leaves, and shoots. Only 7.5 per cent of the twigs were stripped leaving the terminal bud uninjured. There is no significant difference between the two species of willows in the results of browsing.

RATE OF MOVEMENT IN FEEDING

The rate of movement while feeding is characteristic of different species of animals. The white-tail deer, for example, nip here and there with very little pause at any one place. Moose, however, are not of such a nervous temperament and when undisturbed may remain in one clump of willows for several days, leaving only to drink. One cow remained for about two weeks in the same clump where she had calved. An old beaver canal partially filled with water came up to the edge of the clump so there was no necessity for her to go farther to drink.

By the time she left the copse on July 5 all of the twigs within reach had been so severely browsed that many of them were dying.

Another cow that calved very late in the season (June 28, 1948) likewise remained in an area of about two acres for ten days. When disturbed she would simply move from one clump to another.

Thirty-six feeding moose were kept under observation for a total of 1,045 minutes in order to determine their rate of movement while browsing on willows. The distance moved in a five minute interval was estimated. The results obtained from the sample show that in each five minute interval a moose will move an average of three yards, with a range of one to six yards, while feeding undisturbed on willows. Cow 8–7 was observed on August 22, 1948 to feed for twenty minutes without moving more than eight or ten feet; however, this cow had suffered an injury in some unknown manner to her left hind leg and moved about with considerable difficulty.

No appreciable difference in rate of movement was noted whether feeding in the open, or the edge of a clump, or in the center of a clump. The density of growth in the center of a clump of willows offers some resistance to movement, but with an animal as large and as powerful as a moose it apparently is not great enough to hinder them appreciably in moving about. The same rate of movement was observed whether feeding on the low, densely growing *S. Wolfii* or *S. Geyeriana.*

When disturbed by tourists, or if I came too close, or surprised them suddenly, the pattern of feeding behavior of the moose frequently changed. Almost invariably when surprised, the moose would pause long enough to survey the situation. They did not dash away madly without knowing what the danger was. Very frequently the cows would pinch their hind legs together and urinate on them before running. Bulls did not show this manifestation of alarm. Murie (1934) suggests that this may be a reflex action induced by fright. No other explanation seems to be plausible.

If frightened early in the feeding period the moose would move away to a different spot and commence feeding again, whereas if disturbed late in the feeding period they would be more apt to cease feeding altogether and seek out their bedding areas. The more nervous animals would leave the feeding grounds without lingering; others would move off more or less leisurely, feeding as they went.

While feeding in the streams on aquatic vegetation movement is necessarily very slow. There are two types of streams on the study area. One is Obsidian Creek which is swift, cold, and shallow enough that it can be waded easily. However, here and there holes can be found as much as six feet deep. In places where the water is shallow, six inches to two feet, and where it is not too swift the following plants are found growing: *Heteranthera dubia, Nymphaea polysepala, Myriophyllum* sp., *Potamogeton alpinus, P. pectinatus, Utricularia vulgaris, Glyceria pauciflora,* and *Chara* sp.

All of these aquatic plants grow in soft mud of the stream bed, except *Glyceria pauciflora,* which grows on a coarse gravel bottom. In feeding on the muddy stream bed the moose sink into the mud so that the water reaches belly height.

The other type of stream is the slow, more or less stagnant, intermittent stream, some of which may be a part of the canal system constructed by beavers in former times. During late summer many dry up completely, especially the old canals. The bottoms are soft, moose sinking in the mud as much as three feet. The water, however, is quite shallow, averaging six to twelve inches deep. The same species of plants as listed above grow in this type of stream with the exception of *Glyceria pauciflora.* In addition to the plants just listed, the alga, *Spirogyra* sp., is found in the more stagnant pools late in the summer. No moose was seen to eat *Spirogyra,* but Mr. Rudolph Grimm, a

ranger of the park, states that in the winter he frequently has seen them eat it from the streams that are kept open by the run-off from hot springs and geysers. Townsend and Smith (1933) cite observations to show that this alga is actively sought by white-tailed deer of the Adirondacks. They state that in one afternoon twenty-four white-tails were seen in an area of about thirty acres feeding on an alga that was thought to be *Spirogyra*. It is not unreasonable to presume that, in time of low food supply it may figure more prominently in the diet of the moose than was observed in my study.

Because of the impediment offered by depth of water and soft bottoms and also by the relatively concentrated supply of aquatic vegetation as compared with willow the rate of movement in aquatic feeding is very slow. One moose was observed to feed twenty minutes, and another for fifteen minutes, without moving more than three feet. In one instance where the vegetation was sparse another moose moved one yard in three minutes. The average rate of moving while feeding on aquatics was 0.1 yard per minute. This figure was obtained from seventy-three minutes of observation on six different moose.

Height of Browsing

To determine the height at which moose browse on willows in summer feeding, data were gathered in the following manner. After an animal had finished feeding in a clump the height of randomly selected twigs was measured and recorded in the following height intervals in feet; 0.75–1.9; 2.0–3.9; 4.0–5.9; 6.0–7.9; 8.0–9.9; 10.0–11.9. The twigs to be measured were randomly selected by setting up vertical lines every two feet and counting all freshly browsed twigs six inches on either side of that line from the ground to the top of the clump. There were as many places from which measurements were taken in the center as at the periphery of the clump. There proved to be no difference of statistical significance between the amount of browsing done at the edge and in the center in the clumps from which the data were gathered. There may be a greater concentration on the peripheral layer in *S. Wolfii* if the clump is particularly dense and if the brooming effect has been such that short, stiff branches are produced that may be resistant to penetration by the prehensile lip and extremely flexible tongue of the moose. These data were gathered from eleven different moose and are summarized in Table IV.

Table IV. *Height of browsing on willows by eleven adult moose*

Ht. in feet	*S. Geyeriana*		*S. Wolfii*	
	Browsed twigs counted	Per cent	Browsed twigs counted	Per cent
0.75– 1.9	117	16.5	191	33.0
2.0 – 3.9	325	45.7	388	67.0
4.0 – 5.9	246	34.6		
6.0 – 7.9	23	3.2		
8.0 – 9.9	0	0		
10.0 –11.9	0	0		

A total of 711 twigs was measured for *S. Geyeriana* and 579 for *S. Wolfii*, a sufficient number in each case to yield statistically significant results. In *S. Geyeriana* 80 per cent of the browsing occurs within a four foot vertical range and two-thirds of all browsing of *S. Wolfii* occurs within a two foot range. The mean height of browsing on *S. Geyeriana* is 3.49 ft. and for *S. Wolfii* it is 2.34 ft. with standard deviations of 0.48 and 0.93 ft., respectively.

Even though *S. Geyeriana* reaches a height of twelve feet no browsing during the summer was ever seen to occur above seven, however, browsing is evident as high as twelve feet on some willows. It is believed that when browsing occurs above seven feet it is done in winter when snow forces the pliant shoots toward the ground, or if the snow is sufficiently crusted, the moose may be able to walk on top of it. In summer feeding the moose were not seen to "ride" down the

shrubs or to break them off as Murie (1934) observed on Isle Royale.

Table IV shows that the greatest amount of browsing occurs in the 2–4 ft. height interval. With *S. Wolfii* the maximum height falls within this interval and the greatest amount of browsing on this species occurs in the upper third or peripheral layer of the clump. In *S. Geyeriana* there is a greater variability of height of browsing because of the greater height of the plant and as the height increases there is a greater relative amount of browsing in the lower part of the willow where it is more easily taken by the moose. Willows are not browsed at greater heights during summer because of the greater availability of foliage at more convenient levels. Concentration of previous browsing within a relatively narrow vertical range on the shrub has caused the brooming effect to be more pronounced there than at other levels. Up to a certain point the increase in lateral branches would tend to produce a greater foliage at that level. It is suggested that possibly moose would be more strongly attracted to browse at that level because of the increased amount of forage, thus setting up a vicious cycle that tends to concentrate browsing.

Characteristic feeding habits are to some extent dependent on the size and general morphology of the animal. In general the larger the animal the greater would be the range in height from which food could be obtained from a tree or shrub. Moose, being the largest member of the deer family, are able to obtain food from ground level to as high as ten or twelve feet if necessity demands. Possibly the pendant and highly flexible upper lip of the moose is one factor which causes the moose to be a browsing, rather than a grazing animal. Allee *et al.* (1949, p. 241) indicate a possible relationship between the flexible lip structure and browsing habit in the black rhinoceros and elephant of South Africa as contrasted with the grazing habit of the white rhinoceros which possesses square lips.

Peripheral and Central Browsing

In order to determine whether there was any preference exercised for browsing either the edge or the center of a clump, approximately 750 unbrowsed twigs were marked with weatherproof tags on September 1, 1947. The tags were equally distributed between shoots in the outer four feet of the clump and the center. The outer four feet were chosen arbitrarily as defining the periphery because moose and elk can easily browse in that far from the edge without penetrating the clump. The size of the copse chosen for tagging was approximately twenty-five by seventy-five feet and was made up entirely of *S. Geyeriana* ranging in height from three to six feet. The tags were widely scattered throughout the clump so as to preclude the possibility of all tagged shoots being browsed by any one animal at any one time.

The plot was examined on June 9, 1948 to see if any preference had been exercised in browsing. There is no positive way of determining how much of the browsing was done by moose and how much by elk. The question to be answered was simply whether the willow clumps suffer greater browsing at the edge, where feeding appears to be easier, or in the center where movement would seem to be more difficult. The effect on the willows for all practical purposes would be the same if done by elk or if done by moose.

The results of checking the plot showed that in the periphery 13.1 per cent of the tagged twigs had been browsed, while in the center 9.3 per cent had been browsed. The difference in the amount of browsing done in the edge of the clump over that done in the center proved not to be statistically significant.

It was planned to check the plot again at the end of the summer of 1948 but within a space of several days beavers cut most of the shrubs that bore the tags at

the edge of clump, thus making further comparison impossible.

The results of the experiment, findings concerning rate of movement of moose while feeding willows, and observations on feeding elk tend to support each other. The fact that there is no apparent selectivity of location within a clump where browsing may occur indicates that density of willow growth offers no impediment to feeding. For the period concerned, the indications are that both the edge and center of a clump are browsed about equally; however, as pointed out elsewhere, factors such as elk feeding in a compact group, and depth of snow may, over a longer period, cause the shoots at the edge of a clump to be browsed more severely than more centrally located ones.

Summary

A study of the feeding habits of moose was conducted in a limited area of northwestern Yellowstone Park during the summers of 1947, 1948, and 1949. The following conclusions can be drawn:

1. Approximately 88 per cent of the food consists of willow browse; 9.3 per cent consists of aquatic plants; the remainder of the diet is made up of forbs and sedges.

2. Because of the character of the streams in this area, underwater feeding is of little importance.

3. Moose came regularly to mineral licks for the chlorides and sulfates of sodium and calcium contained in the soil. Iron was present in the soil, but it is doubtful if this attracted the moose.

4. In feeding on willows, the moose removes the tender browse by either nipping off the end of the twig, by stripping the small lateral twigs and leaves, or by stripping the lateral twigs and nipping the terminal as well.

5. While feeding undisturbed a moose moves slowly taking a few mouthfuls from one place and some from another. The average rate of movement is three yards every five minutes. When feeding on aquatic vegetation the moose moves more slowly; depth of water, character of stream bottom, and abundance of the food sought, determine the rate of movement.

6. The height through which moose will feed varies from grazing at ground level to browsing as high as seven feet. About 56 per cent of all browsing is done at a level between two and four feet. Willows may be browsed higher in winter.

7. There is no significant difference in the amount of browsing done at the edge of a copse and in the center.

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VEGETATION TYPES IN NORTHWESTERN ALASKA AND COMPARISONS WITH COMMUNITIES IN OTHER ARCTIC REGIONS

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INTRODUCTION

In making surveys for reindeer winter lichen range in northwestern Alaska, a classification of the major kinds of vegetation was needed to show relationships between the distribution and abundance of lichens and the major types which could be readily distinguished on the ground or from the air. Previous classifications, of arctic vegetation, such as those used by Polunin (1934, 1935, 1948), Porsild (1937, 1951), Shelford and Twomey (1941), Palmer (1945), Hopkins and Sigafoos (1951), Seidenfaden and Sørensen (1937), Sørensen (1941), Trapnell (1933) and Hanson (1951) have usually been based upon topographic location, physiognomy, and major constituent species. Shelford and Twomey (1941), Holttum (1922), Oosting (1948), and Hanson (1951) used successional sequences to some extent. Raup (1941) summarized many of the difficulties in the delimitation of arctic plant communities and in the determination of successional relationships. Scandinavians, such as Du Rietz (1925b, 1930), Nordhagen (1928, 1936, 1943), and others have used topographic location, physiognomy, and major constituent species for delimiting the chief geographic communities, and they also have used data from sociological analyses for precise classifications to include orders, alliances, associations, and sociations. They also have included descriptions of habitats and successional relations. Sociological analyses and the classification based on them make it possible to determine the degree of similarity between communities studied in the same way in various parts of Scandinavia, the Alps, and elsewhere. Nordhagen (1943) stated that many things indicate that parallel alliances and orders can be established for Europe and North America. It is hoped that the present article will contribute towards the establishment of a classification applicable to the entire Arctic zone, but it should be emphasized that a vast amount of detailed work, especially in North America, is needed before this can be done.

No suitable classification for the surveys was found, so one was devised comprising 6 major groups and 22 minor groups, or types, based on physiognomy and important constituent species. These 22 types can usually be recognized from the air, preferably when flying at low altitudes as 200 to 500 feet above the ground and at about 90 to 100 miles per hour. For many ground studies a more detailed classification may often be desirable. Sociological analyses have been made of a few of these communities by Hanson (1951) and by E. D. Churchill and the author for the present paper. A classification based upon such analyses must await much additional field work. The classification and characterizations of types are based upon field work

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FIG. 1. Map of Northwestern Alaska, showing location of many places mentioned in the text.

during the summers of 1949–1951, in the northwestern part of Alaska, from the lower Noatak and Kobuk Rivers to the region southeast of Norton Sound (Fig. 1). Additional field work in this area, and in other parts of northern and western Alaska, will reveal other types. Similarities of these types to those described by other investigators, particularly in Scandinavia, are discussed.

The writer agrees with Nordhagen (1943) that vegetation is not a chaotic mixture of plants. Reasons for this are that areas, varying in size, commonly occur which are relatively uniform with respect to chemical and physical characteristics, soil moisture, insolation, depth to perennial frost, depth and duration of snow cover, exposure to wind, etc. The species which can grow under the conditions prevailing on each area become established, often gradually, and the species best adapted to the combination of conditions will survive the competition which usually follows establishment. The range in ecological amplitude of arctic species varies considerably, as shown by Løddesøl and Lid (1950) and others. Usually the stand consists of several to many species. Due to the considerable uniformity in the kinds of species and the number of individual plants of each species per unit area (for example, a square meter) throughout the stand, the composition is similar in its

several parts. Variation within the frame of the homogeneity of the stand occurs due to height and mass of constituent species, and to fluctuations from spot to spot in numbers and kinds of individuals.

The "sociation" is the lowest ranking community in the Scandinavian plant sociology. It forms the primary unit in classification in Scandinavia, and has application to Alaska, so some of Nordhagen's views are summarized as follows:

> Stands which belong to the same sociation show a far-reaching agreement with respect to layering and to the dominant species in each layer. The sociation concept symbolises a special biological equilibrium or balance between several or many species with respect to their individuals or shoots (sometimes only one species). This equilibrium in time may become effective over smaller or larger areas, which appear as more or less homogeneous stands or vegetation units, but their vegetation is never absolutely identical. The equilibrium has a more or less permanent character, enduring at least for years; but under man's influence or catastrophes the balance is often upset and then the process of developing a new balance starts. Or a sociation can "dig its own grave" by drying out the soil, etc. Successional series may not be the same for each stand of a sociation. Variation in stands of a sociation is due to difference in the age of stands, a different course of succession, differences in climate or substratum, influence of adjoining stands (vicinismen). The sociation is therefore an abstraction, the stand is concrete. The requirements of agreement of layers and of homogeneity in the stands of a sociation cannot be set on too rigorous a basis, but must fit natural conditions. Each sociation has its own range of amplitude (1943, pp. 41–44).

Palmer and Rouse (1945) noted little change in many permanent quadrats over periods of 4 to 11 years in northwest Alaska; in others changes occurred due to trampling, grazing, for unknown reasons, etc. Denuded quadrats were usually revegetated by the same kinds of species which had occurred previously. The writer has noted reinvasion by neighboring species on bare spots produced by frost action in dwarf shrub types, and others, apparently soon repairing the damage; but measurements and photographs of permanent sample areas over many years are needed for precise data on the rate of reinvasion and other changes. Except for the limited work by Palmer and associates, such data are lacking for Alaska arctic vegetation.

In 1949 cover and frequency were determined by the point-contact method (Hanson, 1951). In 1951, the method was changed so that the data could be compared directly to those of the Scandinavians and other Europeans. The sociological analyses were made by estimating herbage cover of each species in 10 one-meter-square quadrats located at regular intervals on a line through the stand. The Hult-Sernander scale (Braun-Blanquet 1932, Nordhagen 1943) of cover was modified so that in the records 1 denotes herbage cover of less than $\frac{1}{16}$ of the area of the square meter, 2—$\frac{1}{16}$ to $\frac{1}{8}$, 3—$\frac{1}{8}$ to $\frac{1}{4}$, 4—$\frac{1}{4}$ to $\frac{1}{2}$, 5—$\frac{1}{2}$ to $\frac{3}{4}$, and 6—$\frac{3}{4}$ to $\frac{4}{4}$. The data in the tables can be compared directly to those of the Scandinavian workers by changing "6" to "5."

Preliminary Classification of Vegetation Types in Northwestern Alaska

I. Forest Types
   1. White spruce-shrubs (*Picea glauca-Salix-Betula-Alnus*)
   2. White spruce-Alaska white birch-shrubs (*Picea glauca-Betula resinifera-Salix-Betula-Alnus*)
   3. Alaska white birch-shrubs (*Betula resinifera-Salix-Betula Alnus*)

II. Shrub Types (2.5 or more feet high)
   4. Willow types:
      A. Feltleaf willow (*Salix alaxensis*)
      B. Greenleaf willows (*S. richardsonii, S. pulchra, S. fuscescens*)
   5. Alder types (*Alnus crispa, A. fruticosa*)
   6. Willow-alder-balsam poplar (*Salix-Alnus-Populus tacamahaca*)
   7. Birch types (*Betula nana exilis, B. glandulosa,* and hybrids)

8. Birch-willow types (*Betula-Salix*)

III. Dwarf Shrub Types (less than 2.5 feet high)

9. Dwarf birch-heath-lichens (*Betula nana exilis-Ericaceae-Lichenes*)
10. Blueberry-heath-lichens (*Vaccinium uliginosum-Ericaceae-Lichenes*)
11. Four angled heather-blueberry-mosses (*Cassiope tetragona-Vaccinium uliginosum-Musci*)
12. Alpine bearberry-mountain cranberry (*Arctostaphylos alpina-Vaccinium vitis-idaea*)
13. Alpine dryas (*Dryas octopetala*)

IV. Dwarf Shrub-Marsh Types

14. Cloudberry-dwarf shrub-marsh (*Rubus chamaemorus-Betula nana exilis-Ericaceae*)

V. Herb-Dwarf Shrub Types

15. Alpine sedge-alpine dryas (*Carex-Dryas octopetala*)
16. Cottongrass-sedge-dwarf heath shrub complex (*Eriophorum spissum-Carex-Betula nana exilis-Ericaceae*)

VI. Herb Types

17. Sedge marshes, saline and fresh water (*Carex*)
18. Sedge Sphagnum-moss bogs (*Carex-Sphagnum-Musci*)
19. Grasslands (*Calamagrostis canadensis, Festuca altaica, Arctagrostis latifolia, Elymus mollis, et al.*)
20. Aquatic types (*Hippuris vulgaris, Ranunculus pallasii, Carex aquatilis, Scripus, et al.*)
21. Lichen-moss barrens (*Lichenes-Musci*)
22. Ruderal (*Calamagrostis canadensis, Epilobium angustifolium, Artemisia, et al.*)

I. Forest Types

1. *White spruce-shrubs (Figs. 2, 3)*

Shrubs, 4 to 8 feet high, which may be associated with the white spruce (*Picea glauca* (Moench) Voss.), are willows, birches, alders, spiraea (*Spiraea beauverdiana* Schneid.), currant (*Ribes*), rose (*Rosa acicularis* Lindl.), shrubby cinquefoil (*Potentilla fruticosa* L.), and ericaceous shrubs. A variety of herbaceous plants also occur, including *Calamagrostis canadensis* (Michx.) Beauv., *Festuca altaica* Trin., *Epilobium angustifolium* L., *Mertensia paniculata* (Ait.) G. Don., *Equisetum* spp., and ferns. In the openings and where the shade is not too intense, lichens, chiefly *Cladonia* spp. and *Cetraria* spp., 2 to 5 inches high, and mosses form tufts and mats, as in the vicinity of White Mountain and Council. In places where the stand is fairly open as near Shungnak and on the south side of the Waring Mountains, the lichens form continuous cover over extensive areas (Fig. 2). The white spruce-shrubs type occurs as far west as the valleys of the Noatak and Kobuk Rivers, into the southeastern part of the Seward Peninsula as far as the vicinity of Council, and to within less than a mile of the eastern shore of Norton Sound. West and north of Council, the white spruce appears to be migrating westward.

The forest affords protection to reindeer and caribou from winds during the winter, but herding of reindeer is difficult, and wolves have greater opportunity to seize their prey. The snow may not crust over so badly as in the open. If not shaded too much, reindeer lichens grow well in the forest because they remain moist for a longer time between rains. Fruticose lichens growing on trees afford emergency feed when the snow is excessively deep or a snow crust prevents the reindeer from pawing through to ground lichens (Hanson 1952).

This type is easily recognized from the air by the dark bluish green color and the spire-like growth of the spruces, the dark green masses of shrubs forming a lower layer. The lichens in the openings are conspicuous by their light gray to cream color.

FIG. 2. The white spruce-shrubs type, bordered by shrub types. In the treeless areas are dwarf shrub types and the cottongrass-sedge-dwarf heath shrub complex. White areas are lichens. South slope, Waring Mts., June 30, 1951.

2. *White spruce-Alaska white birch-shrubs (Fig. 3)*

This type was found chiefly along the Unalakleet and other rivers east of Norton Sound, and in places in the valleys of the Kobuk and Noatak Rivers. In the forest northwest of Moses Point Airfield a few birch trees are scattered among the spruces. Shrubs, as in the preceding type, form a lower layer. When the stands are not too dense lichens occur as in the preceding type. The birch trees can be distinguished from the spruce by the dark green color and the large, smooth-appearing globular crowns.

3. *Alaska white birch-shrubs (Fig. 3)*

This type, also of limited distribution, was seen on south-facing slopes bodering the Unalakleet River and other streams east of Norton Sound. Associated shrubs are alders, willows, birches, and dwarf heaths. White spruce and balsam poplar (*Populus tacamahaca* Mill.) are scattered in places. The large, rounded crowns of the birch trees (*Betula resinifera* Britt.) are very distinctive from the air. Stands of this type are often too dense to permit good growth of lichens, but in openings the lichens may cover much of the ground and grow to a height of 5 to 6 inches. Stands of this type may alternate with those of the white spruce-Alaska white birch-shrubs type, the latter often on the steeper slopes (Fig. 3).

Palmer (1945) recognized a forest type as comprising "essentially tundra range occupied by spruce and birch" with undercover of chiefly mosses and lichens. Hopkins and Sigafoos (1951) reported the occurrence of isolated stands of *Populus tacamahaca* on the dissected upland on the north and southwest margins of the Imuruk Lake region in the central part of Seward Peninsula. Du Rietz (1925a) classified the forest types of Scandinavia into two main regions, coniferous and deciduous. The former was divided into a northern and southern part, each of which included coniferous forests, deciduous forests, marshes, bogs, and other communities. He stated that the most important tree in the subalpine maritime birch forest region is *Betula tortuosa* Led., with associated tree species, *Alnus incana* (L.) Moench., *Populus tremula* L., *Sorbus aucuparia* L., *Prunus padus* L., and *Salix* spp. Some of these,

FIG. 3. In the foreground is the cottongrass-sedge-dwarf heath shrub complex with more sedge than cottongrass. Medium-dark area at left center is dwarf birch-heath-lichens type. Very dark area on plain near center is alder type, and beyond the alders is a large light-colored area of the feltleaf willow type. White spruce-shrubs type along the river at foot of hill, dense forest on hill is Alaska white birch-shrubs type, open stands are white spruce-Alaska white birch-shrubs type, and in the distance at left the cottongrass-sedge-dwarf heath shrub complex. Unalakleet River valley a few miles east of Norton Sound. June 13, 1951.

such as *Populus* or *Alnus,* may be the sole dominant. Nordhagen (1936) stated that *Betula tortuosa* forests in the subalpine zone in Norway could be divided into 4 alliances according to the composition of the dwarf shrub and herb layer, and that the birch forests in the mountains of Norway form a mosaic of communities differing floristically and synecologically from one another. He (1943) stated that the most important association (in distribution) in the subalpine birch forest was characterized by the constancy of *Vaccinium myrtillus* L. and *Deschampsia flexuosa* (L.) Trin., and often *Juniperus communis nana* Willd. This community requires long-lasting snow cover. Some of the open white spruce-birch stands in the Noatak and Kobuk River valleys resemble the *Betula tortuosa-Empetrum*

FIG 4. View of the Nome River valley about 9 miles northeast of Nome, showing large areas of willow, birch-willow, and birch shrub types. The dwarf birch-heath-lichens type is lighter gray and finer in texture than the shrub types; the blueberry-heath-lichens type is similar to the preceding but darker; large areas of sedge marsh between the shrubs; cottongrass complex on the distant slopes and benches. June 13, 1951.

hermaphroditum Hag.-*Cladonia alpestris* (L.) Rabenh. association of Nordhagen (1943), growing on dry moraines where the snow blows away quickly. There is similarity also between the white spruce-shrubs type in Alaska and the *Picea excelsa* (Lam.) Link. associations in Norway and in the Alps, the latter described by Du Rietz (1924). Nordhagen (1943) described other forest types in the order Aconitetalia, which comprises tall herb meadows in the mountains, and willow brush and birch forest with a tall herb layer.

Fig. 5. Sedge marsh stand on a gentle slope in the Nome River valley about 10 miles northeast of Nome. Scattered hummocks are dark due to cover of dwarf shrubs. Birch-willow and willow shrub stands beyond. July 12, 1951.

II. Shrub Types

4. *Willow types* (*Figs. 3, 4, 5*)

The willow shrub types are divided into two groups: A. The feltleaf willow type (*Salix alaxensis* (And.) Cov. which is grayish green, and B, the greenleaf willow type which is green. The former is widespread, usually occurring on well-drained banks of streams with coarse gravel at a depth of about a foot (Fig. 3), often forming only a narrow zone (Fig. 4). In height this community may vary from less than 5 to over 15 feet. In some places the ground is hummocky. Some of the associated species are balsam poplar, alder, shrubby cinquefoil, grasses, sedges, and mosses. Lichens are usually lacking.

Several species such as *S. richardsonii* Hook., *S. pulchra Cham.*, and *S. fuscescens* And. may dominate singly or in mixture in the greenleaf willow type (Figs. 4, 5). The height varies from about 4 to 8 feet. This type is found throughout northwestern Alaska and in the aggregate covers much land, such as stream bottoms adjacent to the preceding type, steep banks, drainage ways on slopes where there is usually more or less running water. In poorly drained sites, sedges are more abundant; in drier sites, birch shrubs are associated with the willows.

Due to the presence of hummocks,[2] depressions, and channels, the vegetation

[2] Hummock, mound, and tussock are used in this paper similarly to their ordinary meanings. Hummock and mound are small rounded knolls or raised areas of land, usually covered with many plants, and from a few inches to several feet high. The author uses hummock for somewhat elongated areas, mound for more circular ones. A tussock is a tuft or bunch of grass, or grass-like plant such as *Eriophorum*, which is often separated more or less from other plants in the stand, consisting usually of a single plant.

and soil profile vary considerably from place to place. The depth to the frozen ground in the first part of July, on a gentle east-facing slope about 10 miles northeast of Nome, varied from only 9 inches under dense willows to more than 38 inches under a hummock in openings between the willows. Prominent species on hummocks were the grasses *Calamagrostis canadensis* and *Festuca altaica.* Other associated species were various sedges and forbs such as *Rumex arcticus* Trautv., *Sedum roseum* L., *Galium boreale* L., *Anemone narcissiflora* L., *Artemisia arctica* Less., *Dryas octopetala* L., *Mertensia paniculata, Viola langsdorfii* Fisch., and dwarf shrubs including *Empetrum nigrum* L., *Vaccinium uliginosum* L., *Salix reticulata* L., and *Andromeda polifolia* L. The last two, and *Potentilla fruticosa, Woodsia glabella* R. Br., *Sedum roseum, Salix reticulata, Carex aquatilis* Wahl., *Corydalis pauciflora* (Steph.) Pers,. *Polemonium acutiflorum* Willd., mosses, and others occurred in depressions.

The soil profile under dense willows, 8 feet high, on a 5° slope, in this stand which covered several square rods, examined on July 1, 1950, had a layer of loose leaves about an inch thick above a 0.5-inch layer of decayed plant debris. Below this for 9 inches, the silt loam was brown to dusky red, containing much organic matter, except for the 6–7.5-inch layer which contained much fine schist. The roots were numerous to 7.5 inches, then infrequent to the frozen ground at 9 inches.

A hummock only a foot away, covered mostly with grass, had a 2-inch litter layer, below which brown to dark reddish brown silt loam extended to 7.5 inches, containing considerable grayish brown silt loam at 5–7.5 inches. Between 7.5 and 17 inches stones and gravel were interspersed in the gray brown to reddish brown silt loam. From 17 to 38 inches (no frozen ground) the material varied from pale gray silt to grayish brown sandy silt with stones and gravel, the latter increasing with depth, so drainage was excellent. Roots were numerous to 17 inches. The soil reaction, determined colorimetrically by the LaMotte-Morgan Method, was similar in the two profiles, mostly pH 6.2 and 6.4, but the surface 2.5-inch layer in the hummock was pH 5.2.

Palmer (1945: 6) recognized only a "shrub-grass-weed type" occurring "on well-drained ground, usually along a stream, in a ravine or on a steep slope," and included alder with the green willows. Hopkins and Sigafoos (1951: 65) described willow communities in the Imuruk Lake area as follows: "Willow (*Salix pulchra*) thickets 4 to 10 feet high occur in the lower reaches of the swales draining higher slopes, on steep lake banks, and on flood plains of the larger streams. Depth to perennial frozen ground is more than 6 feet, and frozen ground may be absent locally under flood plains. Definite channels of running water are present under the willows in the swales; these channels are among the few sites where erosion by running water is occurring in the Imuruk Lake area." Trapnell (1933) recognized in his provisional classification of vegetation types in the Godthaab Fjord district in Greenland a *Salix glauca* L. community, 1 to 2 m. high, with associated *Alnus incana,* forming a continuous cover, hiding the field layer of grasses, ferns, *Potentilla maculata* Pourr. *et al.,* and a ground layer of typical *Brachythecium* spp. Nordhagen (1943) described 3 associations of willow types, consisting of *Salix lapponum* L., with which *S. glauca, S. lanata* L., *S. phylicifolia* L., and others, may be associated, often over 6 feet high, in the order Aconitetalia and in Order I are willow thickets with a sedge-marsh layer of many species. The 3 associations were distinguished chiefly by differences in the herbaceous species in them. Du Rietz (1925a) stated that these willow thickets, 1 to 2 meters high, are almost impenetrable, covering considerable ground along brooks, or where there is some running

water, in the lower alpine region in the Scandinavian mountains.

5. *Alder types* (*Fig. 2*)

The alder types (*Alnus crispa* (Ait.) Pursh., *A. fruticosa* Rupr.) form dark bluish green thickets on well-drained slopes and bluffs throughout the region, from about 3 to 12 feet high. They are very distinctive because of the dark color and dense masses. A lower layer of herbaceous and shrub vegetation is usually present, often with much *Calamagrostis canadensis*. Other prominent species, especially in the more open stands are *Betula* spp., *Spiraea beauverdiana, Vaccinium uliginosum, Salix* spp., *Cornus suecica* L., *Lycopodium annotinum* L., *Epilobium angustifolium, Pedicularis labradorica* Panz., *Carex* spp., *Hierochloe alpina* (Sw.) R. & S., mosses and lichens. In places, as where alders border streams the lowest parts of the stands may contain many willows. On the edges of stands a dense zone of low shrubs as birches, Spiraea, dwarf heath shrubs, and some herbaceous species such as *Calamagrostis canadensis, Epilobium angustifolium,* and *Petasites frigidus* (L.) Fries may occur. Occasionally alders are scattered in the cottongrass-sedge-dwarf heath shrub complex, as, for example, on slopes north of Unalakleet.

According to Hopkins and Sigafoos (1951), alder thickets are scattered on steep, better-drained slopes in the Imuruk Lake area. Trapnell (1933) reported finding one pure alder shrub thicket in a silted gorge in the Godthaab Fjord district in Greenland. Du Rietz (1925a) pointed out that forests of *Alnus glutinosa* (L.) Gaertn. are common along streams and lakes in the southern coniferous forest region in Scandinavia, and on moraines in the subalpine-maritime birch forest region. The similarity of Alaskan alder stands to an *Alnus viridis* DC. type is indicated in an analytical table by Du Rietz (1924: 47). Nordhagen (1943) mentions an alder association in the subarctic region of Norway as having a dominance of tall ferns (*Struthiopteris* sp. and *Athyrium filix-femina* (L.) Roth.) in the field layer.

6. *Willow-alder-balsam poplar type*

Dense thickets, about 10 to 15 feet high, of a mixture of *Salix* spp., *Alnus* sp., and *Populus tacamahaca* were seen on the flood-plain of the Unalakleet River. It probably occurs along other streams also. From the air it appears dark green.

7. *Birch types* (*Figs. 2, 4, 5, 6*)

These types, consisting chiefly of *Betula nana exilis* (Suk.) Hult., *Betula glandulosa* Michx., *Betula* hybrids, and scattered individuals of *Salix* spp., 2.5 to

FIG. 6. Birch shrub type with intermixed willows in foreground and on lower part of slope across the creek. Large light area is the cottongrass complex, *Eriophorum spissum,* headed out. Coffee Creek, west of Bendeleben Mts., central part of Seward Peninsula. June 23, 1951.

TABLE I. *Birch-shrubs stand, 10 miles northeast of Nome. Aug. 1, 1951*

Species	1	2	3	4	5	6	7	8	9	10	Aver. Cover	Freq. %
Betula nana exilis	5	4	6	6	6−	6	6	5	6	4	5.4	100
Salix richardsonii	1	3				1					2	30
Salix pulchra										4	—	10
Salix reticulata	1	2−	1−			1	1	3			2−	60
Vaccinium uliginosum	3−	3−	2	1	1	1	3	3	1	1	1.9	100
Empetrum nigrum	1	2	1	1	1−	1−	1	1	1	1	1	100
Vaccinium vitis-idaea		1	1	1	1	1	1	1	1	1	1	90
Ledum decumbens	1−	1	1	1	1−	1	1			1	1	80
Arctostaphylos alpina	1−	2	1−				1	1			1	50
Potentilla fruticosa	1−						1		1		1	30
Rubus arcticus					2	1		1−			1	30
Festuca altaica	1−	1−	1−		1−	1+	1−	1−	1−	1−	1−	90
Carex sp.		1		1	1	1−	1	1+	1	1	1	80
Calamagrostis canadensis		1−	1	1−	1	1−	1−	1−	1−		1−	80
Valeriana capitata			1			1−	2	1+	1	1	1	60
Polemonium pulcherrimum						1−	1	1	1−	1	1	50
Arctagrostis latifolia	1		1−		1−	1			1−		1−	50
Poa arctica?					1−		1−		1−	1−	1−	40
Polygonum bistorta plumosum						1−	1−	1	1		1−	40
Botrychium lunaria	1−	1−						1−	1−		1−	40
Arnica porsildiorum	1−	1−	1−								1−	30
Saxifraga punctata			1−				1	1−			1−	30
Papaver radicatum	1−	1−									1−	20
Cardamine pratensis	1−								1−		1−	20
Solidago virgaurea		1−						1−			1−	20
Equisetum scirpoides	1−						1−				1−	20
Pedicularis verticillata						1−		1−			1−	20
Cerastium beeringianum	1−						1−				1−	20
Mertensia paniculata								1−	1−		1−	20
Petasites frigidus									1−	1−	1−	20
Equisetum sp.			1−								—	10
Lycopodium annotinum						1					—	10
Mosses	6	6	6	3	6	6	6	6	6	6	5.7	100
Lichens	1	2	2		2	3	1	1	1	2	1.7	90
No. vascular spp. per m²	16	15	14	6	11	17	18	18	17	12		
Aver. No. vascular spp. per m²	14.4											

about 8 feet high, are widespread in northwestern Alaska. They occur usually on moderate slopes, at lower elevations, and cccupy in the aggregate considerable area. Density varies from open to closed. In the openings and on the edges of dense stands occur dwarf shrubs and herbs, and lichens up to 4 to 5 inches may be dense unless the area has been heavily grazed or burned. The ground within dense stands may be covered with a thick layer of moss with lichens sparse or lacking. From the air these types have a characteristic brownish green color; the gray to cream-colored lichens mats are conspicuous in the openings. This type is a good indicator of conditions suitable for excellent growth of lichens.

A sociological analysis of a stand, occupying an acre of more, similar to that on the right in Fig. 5, on an east-facing slope of about 5°, located about 10 miles northeast of Nome, is shown in Table I. The elevation was about 120 feet above sea-level. The stems of the birch shrubs were usually decumbent for 2 or 3 feet and then gradually ascended to an average height of about 3.5 feet. The lower parts of the stems become covered with an inch or so of moss and litter in which new roots develop. A single shrub may occupy an area as much as 10 feet in di-

ameter with its widely spreading branches. The scattered green willows were often a foot or two taller than the birches. The ground was covered with moss, chiefly *Hylocomium splendens* (Dedw.) Schimp. The most abundant shrub, after the birch, was *Vaccinium uliginosum.* All other vascular species had low cover, but some were high in frequency notably *Empetrum nigrum, Festuca altaica, Carex* sp., *Vaccinium vitis-idaea, Calamagrostis canadensis,* and *Ledum decumbens* (Ait.) Lodd. Important species among the lichens were *Cladonia rangiferina* (L.) Web., *C. sylvatica* (L.) Hoffm., *C. cornuta cylindrica* (Ach.) Asa., *Cetraria cucullata* (Bell.) Ach., and *C. islandica* (L.) Ach.

The soil profile, examined on July 10, 1951, had a surface layer, 2 inches thick, of moist, partly decayed, dark reddish brown plant fragments, with numerous living roots and rhizomes. The 2–9 inch layer was dark brown, wet, silt loam, rich in organic matter, with numerous roots to the working depth at 9 inches. The 9–16 inch horizon was compact, wet, gray to olive-gray silt, highly impervious to water, with included layers and pockets of gray-brown silt loam containing organic matter and pockets of yellow brown silt loam. The heterogeneity in this horizon appeared to be due to solifluction and frost action. Live roots were few and dead roots numerous below 9 inches. The 16–17 inch layer was brown silt with scattered stones. The ground was frozen at 17 inches.

Examination of several profiles in different stands in this vicinity showed the following general characteristics: 1) a moss layer on the surface, 2) a reddish brown organic layer containing little to no silt between the moss and 2 to 4 inches in depth, 3) in some stands, a silty loam layer rich in organic matter from about 2 or 4 inches to 7 or 9 inches, 4) below 9 to 13 inches a mixed up or irregular horizon of impervious gray to brown silt mottled with yellow brown. Schistose rocks become more numerous and compact with depth. The gray silt is like a stiff jelly when wet. Frozen ground was found in one profile at 17 inches, but in others none was found even as deep as the fairly compact schist at 22 and 29 inches. These birch shrub profiles resemble the one in the *Betula glandulosa* stand in Mt. McKinley National Park described by Hanson (1951: 361).

Palmer (1945) apparently included this community in his "lichen-shrub" type. Hopkins and Sigafoos (1951) wrote that thickets of *Betula nana exilis* in the Imuruk Lake area "occur on the better-drained, higher parts of steep banks and well-drained slopes. Depth to perennially frozen ground—is not known—but is probably more than 6 feet—." The birch shrub communities in Alaska are similar to those found in places in the low alpine zone in Norway where the dominant is *Betula nana* L., reaching a height of more than 2.5 feet. They are also similar to types where the dominant is a *Betula* hybrid according to Lagerborg and Holmboe (1938). *Betula nana* is usually less than 2.5 feet high in Norway, so communities dominated by it are probably more similar to the Alaskan dwarf birch-heath-lichen type discussed below. The birch shrub types in Alaska also resemble the "shrub tundra," or "jernik," of northern and eastern Siberia, which are dense communities of *Betula fruticosa* and *B. exilis,* 1 to 1.5 meters high, occurring on marshy lowlands with sedges, and also in dry open glades on slopes, according to Imanishi (1950).

8. *Birch-willow type*

This type is made up chiefly of *Betula glandulosa,* tall forms of *B. nana exilis,* or *Betula* hybrids. It resembles the preceding type, but contains a larger proportion of willows (*Salix pulchra, S. richardsonii, S. fuscescens*), and alders, *Spiraea,* or white spruce may also be scattered throughout. From the air it may appear spotted, due to the pale green willows, the dark blue alders, and the brownish green birches. The shrubs are 6 to 10 feet high,

the white spruce up to 20 or 30 feet. Dwarf shrubs such as *Ledum decumbens, Betula nana exilis, Vaccinium uliginosum, V. vitis-idaea, Rubus chamaemorus,* L. *Oxycoccus microcarpus* Turez., also occur, the last two in more boggy spots with *Sphagnum* and other mosses. Grassy spots are formed by *Calamagrostis canadensis, Festuca altaica, Poa* sp., *Mertensia paniculata, Sedum roseum, Cardamine pratensis* L., *et al.* Lichens, 4 to 6 inches high, form tufts on hummocks, and patches several rods square where the shrubs are scattered. Important species are *Cladonia rangiferina, C. sylvatica, C. cornuta cylindrica, C. gonecha* (Ach.) Asa., and *Stereocaulon tomentosum* Fries. This type was studied particularly in the vicinity of Council where it occupies large areas.

III. Dwarf Shrub Types

Only 5 of the more distinctive dwarf shrub types are described in this paper. They are usually less than 2.5 feet high, widely distributed, cover considerable areas, and can usually be readily recognized from the air. These 5 types are not coordinate in rank, and except for number 11, correspond roughly to major divisions, such as alliances, in the phytosociology of Nordhagen (1943), Du Rietz (1924, 1930), Braun Blanquet (1932), *et al.* Undoubtedly a number of distinct communities (associations and sociations according to the Scandinavian workers) occur in each of types 9, 10, and 13; but much additional field work and sociological analysis are needed for their idetntification, characterization, and classification.

Table II. *Dwarf birch-heath-lichens stand, 10 miles northeast of Nome. July 30, 1951*

Species	1	2	3	4	5	6	7	8	9	10	Aver. Cover	Freq. %
Betula nana exilis	2	1	3	3	3+	3	2+	1	1	3	2.2	100
Vaccinium uliginosum	1	2	3		3+	4	1	4	4+	2	2.7	90
Empetrum nigrum	3	1	4+	1	2		4	2−	2	3	2.3	90
Vaccinium vitis-idaea	1	2	1	1	1	1	2−	2−	1	1	1.3	100
Loiseleuria procumbens			1	1	2		1	3	3	3+	2	70
Ledum decumbens	1	1+	1	1	1	1	1	1	1	1	1	100
Salix pulchra			1						2	1	1	30
Salix alaxensis		1									—	10
Salix reticulata			1					1	1	1−	1	40
Salix richardsonii					1			1		1	1	30
Spiraea beauverdiana					1−						—	10
Pyrola grandiflora?								1	1−		1−	20
Carex montanensis	1−	1−	1−	1−	1−	1−	1−	1−	1−	1−	1−	100
Pedicularis labradorica	1−		1−	1−	1−		1−	1−		1−	1−	70
Festuca altaica	1−	1−			1−	1−			1−	1−	1−	60
Poa arctica				1−	1−		1−	1−		1−	1−	50
Petasites frigida			1−	1−	1−	1−					1−	40
Luzula multiflora			1		1−					1	1−	30
Polygonum bistorta plumosum					1			1			1	20
Solidago virgaurea				1				1			1	20
Lycopodium annotinum				1−			1−				1	20
Cardamine?								1−	1−		1−	20
Calamagrostis canadensis			1								—	10
Agrostis borealis			1								—	10
Hierochloe alpina									1−		—	10
Saussurea angustifolia									1−		—	10
Mosses	2	5	6	6	6	5	5	6	6	6	5.3	100
Lichens	6	4+	5	4+	5	5	3+	2	4	4	4.2	100
No. vascular spp. per m²	8	8	14	11	15	7	10	16	15	15		
Aver. no. vascular spp. per m²	11.9											

Additional species in the stand but not in any quadrat: *Dryas octopetala, Potentilla fruticosa, Lycopodium selago.*

TABLE III. *Dwarf birch-heath-lichens stand, 10 miles east of Nome. July 30, 1951*

Species	1	2	3	4	5	6	7	8	9	10	Aver. Cover	Freq. %
Loiseleuria procumbens	4	4	1	1+	4−	2−	3−	2	4	1	2.6	100
Empetrum nigrum		1−	2	2−		1−	2	2	1	2−	1.6	80
Betula nana exilis	1−	1	1+	1+	2−	2−	1+	1	1+	3	1.4	100
Ledum decumbens	1−	1−	1+	1	1	1	1	2	1	2	1.2	100
Vaccinium vitis-idaea	1	1+	1	1	2−	2−	2+	1	1	1	1.3	100
Vaccinium uliginosum	1		1−	1			2+	1+		1+	1.1	60
Salix pulchra								1			—	10
Salix phlebophylla		1+									—	10
Carex montanensis	1	1−	1	1−	1+	1	1+	1−	1	1	1	100
Hierochloe alpina	1−		1−	1−	1−	1−	1−	1−	1−	1−	1−	90
Pedicularis labradorica			1−	1−	1−		1−	1−			1−	50
Luzula multiflora								1		1−	1−	20
Festuca altaica										1−	—	10
Luzula parviflora							1				—	10
Mosses	1−	1−	1	1	1−	1−	3	3	1	2+	1.5	100
Lichens	6	3	6	6	6	6	5	6	5	6	5.5	100
Bare ground	1	3		1	1−	1−			1−		1	60
No. vascular spp. per m²	8	8	9	10	8	8	10	11	8	10		
Aver. no. vascular spp. per m²	9.0											

Additional species in stand but not in any quadrat: *Arctagrostis alpina, Calamagrostis canadensis Lycopodium annotinum.*

9. *Dwarf birch-heath-lichens type (Figs. 2, 3, 4, 6)*

This type is usually characterized by the abundance of *Betula nana exilis* and by lesser abundance of several kinds of dwarf heath and similar shrubs such as *Vaccinium uliginosum, Ledum decumbens, Empetrum nigrum, Vaccinium vitis-idaea, Loiseleuria procumbens* (L.) Desv., and *Arctostaphylos alpina* (L.) Spreng., by scattered low willows, especially *Salix pulchra,* and *S. richardsonii,* by scattered herbs, and by an abundance of lichens of many species and several kinds of mosses. One or more of the heath shrub species may be more abundant in some stands than the dwarf birch, but the latter is always prominent in this type. The shrubs are usually less than a foot high. The spaces between and under the shrubs are occupied by lichens, 2 to 4 inches high.

The birch-heath-lichens type occurs throughout the region on gravelly and rocky slopes and terraces at lower elevations where the soil is well-drained and dries out rather rapidly after rains. These sites become free of snow early in the season and are probably bare during part of the winter also. Stands of this type are conspicuous from the air because of the short and scattered shrubs with the carpet of yellowish gray to gray lichens beneath. Microstands of this type are found on hummocks and mounds in other communities, as, for example, in the cottongrass-sedge-dwarf heath shrub complex, sedge marshes, etc. Where the lichens have not been depleted, it is valuable for winter and spring range for reindeer.

Analysis is given in Table II of a fairly typical stand of this type, and in Table III of a similar stand on shallower soil, each comprising several square rods. The latter stand might more appropriately be called a *Loiseleuria procumbens-Cladonia* community, or according to the Scandinavian system, a sociation in the dwarf birch-heath-lichens alliance. In the first there were 37 vascular species, in the latter only 14. The latter was much less dense, bare ground occupying 1/16 of 6 of the quadrats, and the vascular plants were about half as tall as in the first, averaging about 6 inches. The average number of species

per quadrat in the first was 11.9, in the second 9.0. The chief kinds of vascular species in the first in order of high cover and frequency were *Betula nana exilis, Vaccinium uliginosum, Empetrum nigrum, Loiseleuria procumbens,* and *Vaccinium vitis-idaea*; in the second *Loiseleuria procumbens, Empetrum nigrum, Betula nana exilis, Vaccinium vitis-idaea, Ledum decumbens,* and *Vaccinium uliginosum.* The chief herbaceous plants in the first were *Carex montanensis* Bailey, *Pedicularis labradorica, Festuca altaica,* and *Poa arctica* R. Br.; in the other *C. montanensis, Hierochloe alpina,* and *Pedicularis labradorica.* Mosses had three times more cover in the former as in the latter; lichens about 25 per cent more cover in the latter. Lichens present in both stands were *Cladonia rangiferina, C. sylvatica, C. pleurota* (Floerke) Schaer., *C. cornuta cylindrica,* and *Cetraria cucullata*; they were taller and denser in the first stand. The following lichens were more common in the second stand: *Stereocaulon tomentosum, Cladonia macilenta squamigera* Vain., *C. delessertii* (Nyl.) Vain., *C. pleurota, Pertusaria coccodes* (Ach.) Nyl., *Pilophorus cereolus* (Ach.) Th. Fr., *Thamnolia vermicularis* (Sw.) Schaer., and *Nephroma arcticum* (L.) Torss. The more common mosses were *Polytrichum piliferum* Hedw., *Hylocomium splendens, Drepanocladus uncinatus* (Hedw.) Warnst., *Ptilidium ciliare* (L.) Nees., and *Bryum* sp. The moss-like *Selaginella selaginoides* (L.) Link. was also common.

Differences in the kinds of species and in their cover and frequency in these two stands can be explained largely by differences in the soil profiles. In general there was less silt and more rock close to the surface in the soil underlying the thin stand. The reaction in both was acid, with pH 4.6 to 5.0. Beneath the 2-inch layer of moss, lichens, and plant parts in the denser stand (Table II) was a 4-inch horizon of dark reddish brown silt, rich in organic matter, containing very many roots in the upper half. Between 4 and 7 inches, the brown silt was interspersed with many small, thin schistose stones, and the roots were frequent to the working depth at 7 inches. At 7–11 inches the grayish brown sandy silt, containing much gravel, was like a stiff jelly, tending to flow off the wall into the hole. Roots were infrequent. At 11–20 inches was pale brown, sandy silt, with gravel and small thin stones which increased in number and size with depth, so that at 20 inches there was more rock than silt. The roots were scarce.

A 2-inch layer of lichens and mosses covered the ground under the sparse stand (Table III). Below this was a horizon, varying in thickness up to 2 inches, which consisted of loose, dark brown, decayed plant debris with a few schist flakes and very numerous roots. Below this to about 5.25 inches was dark reddish brown silt loam with much organic matter, much more compact than the layer above, containing scattered gravel and schist pieces; the roots were infrequent. Between 5.25 and 14 inches was mostly loose, crumbling pieces of schist, with few roots. Palmer and Rouse (1945) stated that the stand of this type in the Dexter Creek area, 8 miles north of Nome, showed little change between 1922 and 1932. Quadrats which had been denuded became revegetated by the same species originally on the quadrats. They estimated that it would probably take about 25 years for the vegetation to return to the original condition of density, cover, and volume. When this area was examined by the writer in 1950 and 1951, the vegetation, except for reduced height growth of lichens due to grazing and trampling by reindeer, was similar to that described by Palmer and Rouse as occurring on the site in 1922. This type seems to have considerable permanence.

Dwarf birch-heath communities were included by Palmer (1945) in the "dry tundra type" and by Porsild (1951) in "dwarf shrub-heath" community in the "tundra" group. Oosting (1948:249) recognized in a general way various kinds of communities in the heath type in northeast Greenland, stating that *Betula nana* "may become a dominant in sheltered or

southern exposures of heath vegetation and especially on sites somewhat drier than the more widespread *Vaccinium* heath." Trapnell (1933) described and illustrated dwarf birch-lichen and *Ledum*-dwarf birch types in the Godthaab Fjord region which show much resemblance to communities in the Nome district. Du Rietz (1925a) discussed briefly various dwarf shrub-heath communities in the lower alpine region, the *Betula nana* heath resembling the type in Alaska. He stated that the lichen-rich areas in Scandinavia are the driest sites, while in the Alps the lichen-rich dwarf shrub-heath sites are the most moist. Du Rietz (1925b) pointed out that C. E. Fries in 1913 was the first to thoroughly characterize a large number of dwarf shrub heath associations in Scandinavia. Mosses and lichens, according to Du Rietz, Nordhagen, and others, are more sensitive to environmental conditions than dwarf shrubs and herbs. On the basis of both ground and field layers, he classified dwarf shrub heath communities into 3 major groups: 1) lichen-rich, 2) naked, poor in lichens and mosses, and 3) moss-rich. The stands in the Nome district discussed in the present paper show much resemblance to Du Rietz's (1925b) *Betula nana-Cladonia rangiferina-silvatica* association, which he stated is also important in the Alps. Nordhagen (1943) included in his Order A, dwarf shrub heath on lime-poor rock, two alliances, 7 associations, and 14 sociations. These communities occurred as a lower story in the spruce-pine and birch zones, as well as without a tree layer in the low alpine region. The stand analyzed in Table II shows most resemblance to his association number 4, dwarf birch-*Empetrum* heath. The stand analyzed in Table III resembles more his association number 1, *Loiseleuria* heaths. Both of Nordhagen's associations are important as reindeer range, often snow-free in winter, especially the latter community.

Another small stand of 1 or 2 square rods, resembling even more closely Nordhagen's association number 1, was examined on stony, gravelly sites on the ridge at Golovin. The sparse vegetation consisted of *Loiseleuria procumbens, Arctostaphylos alpina,* short lichens and mosses, and invading plants of *Ledum decumbens, Empetrum nigrum,* and *Betula nana exilis.* It appears that *L. procumbens, A. alpina,* and *Salix phlebophylla* And. become more abundant, and *B. nana exilis* and *Vaccinium* spp. less abundant in more rocky and gravelly soil and at higher elevations, such as at 500 feet on King Mountain north of Nome and at Salmon Lake. On a gravelly outwash, several acres in area, on the north side of Salmon Lake, the following species were abundant: *Loiseleuria procumbens, Salix phlebophylla, Vaccinium vitis-idaea,* and *Arctostaphylos alpina*; frequent: *Rhododendron kamtschaticum* Pall.; infrequent to scarce: *Betula nana exilis, Ledum decumbens, Vaccinium uliginosum, Salix chamissonis* And., *Carex* sp., and *Campanula uniflora* L. Mosses, especially *Polytrichum* sp., and short lichens of many kinds were abundant.

Nordhagen stated that *Betula nana* does not tolerate long-lasting snow-cover, shade, or unstable slide sites. It dominates on infertile gravel and sand deposits with acid humus or with extremely acid peat. It can raise itself better than any other dwarf shrub above compact lichen masses, so that only the tops of the shoots project above them.

10. *Blueberry-heath-lichens type* (*Fig. 4*)

This type resembles the preceding one, but blueberry (*Vaccinium uliginosum*) is the chief dominant, often forming very dense stands. *Betula nana exilis* is much less abundant, and when present is often very short and scattered. *Empetrum nigrum* and *Ledum decumbens* are more numerous usually than in type 9. Other important dwarf shrubs are *Vaccinium vitis-idaea, Loiseleuria procumbens, Salix pulchra,* and *Arctostaphylos alpina.* Herbs, such as *Luzula, Calamagrostis canadensis, Festuca altaica, Carex, Valeriana capitata* Pall., and *Pedicularis capitata* Adams are scattered. Mosses are generally distrib-

uted. Lichens are more spotted in occurrence than in type 9, the shrubs often being too dense for their growth. In shorter, more open stands, however, lichens may cover 75 per cent of the ground. This type occurs on gentle to steep slopes where gravel and rocks are close to the surface, but the sites are moister than in type 9. While it is found at the same elevations as the dwarf birch-heath-lichens type, it also covers large areas at higher elevations, as 400 to 500 feet or more north of Nome, elevations where the dwarf birch type is lacking. The snow probably remains later than in the dwarf birch type, but not so late as in type 11 where there is more *Cassiope tetragona* (L.) D. Don.

The blueberry-heath-lichens type is widespread in hilly parts of the Seward Peninsula, and is conspicuous from the air because of its dark bluish green color, with the gray of the lichens interspersed in spots, and because of the smooth texture. When not damaged by overgrazing or fire it is valuable for winter grazing by reindeer. Stands intermediate between types 9 and 10 were found, but their status cannot be definitely determined until sociological analyses are available.

Palmer (1945) included stands of *Vaccinum* spp. and associated species in his "dry tundra type." Oosting (1948) recognized a heath type dominated by *Vaccinium uliginosum microphyllum* (Lge.) Nath. in northeast Greenland, especially inland on sandy slopes with associates *Empetrum nigrum* and *Arctostaphylos alpina*. Trapnell (1933) also refers to communities dominated by *V. u. microphyllum* in Greenland. Seidenfaden and Sørensen's (1937) ecosystem on "moderately moist sheltered precipices and rock ledges," especially at heads of fjords, in northeast Greenland, was dominated chiefly by *V. uliginosum*. *Salix arctica* was another dominant, and associated species were *Dryas octopetala* on upper dry areas, and *Cassiope tetragona* on lower moist areas. Also present were *Rhododendron lapponicum* (L.) Wahl., *Empetrum nigrum*, and several herbs. He wrote that this type is supplied with water until late in the summer, and that *V. uliginosum* "within our areas can be said with no little right to replace *Betula nana* of the somewhat more southerly areas" (p. 121). Du Rietz (1925a) stated that *V. uliginosum* heath plays an important role on wind-exposed slopes, without solifluction terraces, in the lower alpine zone in Scandinavia. Du Rietz (1924) showed similarities in *V. uliginosum* communities in Scandinavia and in the Alps. Some of the species present in both locations, as well as in Alaska, were *Empetrum nigrum, Loiseleuria procumbens, Vaccinium vitis-idaea,* and others. The Alaskan type is similar to Nordhagen's (1943) low alpine *Vaccinium uliginosum* heath (association number 2), and the low alpine *V. myrtillus* heath (number 8), the latter occurring where the snow lies late.

11. *Four-angled heather-blueberry type*

This type shows relationships to the preceding type, but occurs where the snow lies later. It is found on hilly sites throughout the region. The dominant dwarf shrubs are *Cassiope tetragona* and *Vaccinium uliginosum*, but *Empetrum nigrum* also rates high in frequency and cover. An analysis of a stand about 8 miles north of Nome is given in Table IV. Additional dwarf shrubs in this stand were *Dryas octopetala, Salix reticulata, S. chamissonis, Betula nana exilis,* and *Ledum decumbens*. The herbs with the highest cover and frequency were *Carex* sp., *Festuca altaica, Polygonum bistorta plumosum* (Small) Hult., *Equisetum scirpoides* Michx., *Pedicularis verticillata* L., and *Hedysarum alpinum americanum* Michx. Mosses formed a layer over the ground. Lichens, 1 to 3 inches high, were widely distributed but sparse, usually not sufficient for winter range. The ground was completely covered with vegetation, usually with two layers. The total number of species in the ten m^2 quadrats was 32, the average number per quadrat 15.5, both figures larger than in most stands. In some stands, where

TABLE IV. *Heather-blueberry-moss stand, 8 miles north of Nome. Aug. 1, 1951*

Species	1	2	3	4	5	6	7	8	9	10	Aver. Cover	Freq. %
Cassiope tetragona	3+	3+	5+	4	4	3	4	4+	4−	4−	3.8	100
Vaccinium uliginosum	5−	5−	2	3	3	3	3	3	3	4	3.4	100
Empetrum nigrum	2	3	3	3+	3−	3−	2	1	3	3	2.6	100
Dryas octopetala	2	1	1	1	1	3	2	1	2−	1	1.5	100
Salix reticulata	1	1		1	1	2	3	1−	2	1	1.5	90
Salix chamissonis	1	1	1+	1	1+	2		1		1	1.1	80
Betula nana exilis			1−	2	1	1					1	40
Ledum decumbens						1−					—	10
Carex sp.	1−	1	1	1	1	1	1+	1	1	1	1	100
Festuca altaica	1−	1−		1−		1	1−	1	1−	1	1−	80
Polygonum bistorta plumosum	1−	1	1	1			1−	1−	1	1−	1−	80
Equisetum scirpoides	1−	1−	1	1−		1−	1−	1−			1−	70
Pedicularis verticillata					1	1−	1−	1−	1	1−	1−	60
Hedysarum alpinum americanum	1−		1−	1−			1		1−	1	1−	60
Dodecatheon macrocarpum	1+					1		1	1−	1	1	50
Calamagrostis canadensis		1−	1−			1−	1−		1−		1−	50
Cerastium beeringianum	1−			1−					1	1−	1−	40
Anemone narcissiflora	1					1−		1−		1−	1−	40
Pyrola minor								1−	1−		1−	20
Polygonum viviparum	1			1−	1−		1−				1−	40
Equisetum arvense	1−				1−				1−	1−	1−	40
Arnica porsildiorum		1−	1−						1−		1−	30
Artemisia arctica						1−		1−		1−	1−	30
Cardamine pratensis						1−			1−	1−	1−	30
Papaver radicatum	1−	1−							1−		1−	30
Valeriana capitata								2	1−		1	20
Luzula multiflora	1−										—	10
Equisetum sp.	1−										—	10
Saxifraga hieracifolia									1		—	10
Claytonia sarmentosa						1−					—	10
Saussurea angustifolia								1−			—	10
Lycopodium annotinum										1−	—	10
Mosses	6	6	6	6	6	6	6	6	6	6	6	100
Lichens	1−	2	2	3	3	4	1	1	1	1+	1.9	100
No. vascular spp. per m²	19	13	12	14	11	18	13	17	20	18		
Aver. no. vasc. spp. per m²	15.5											

Additional species in the stand but not in any quadrat: *Polemonium pulcherrimum, Saxifraga hirculis, Salix alaxensis.*

snow apparently melts later, *Cassiope tetragona* is the sole dominant. From the air this type appears dark bluish green, even darker than type 10, and smooth in texture. Occurring more in depressions it often alternates with stands of the dwarf birch-heath-lichens type on exposed ridges, and with taller shrubs, especially willows in deeper draws. In some draws, where the snow does not melt until in July, meadow-like stands occur in which the following are abundant: *Rhododendron kamtschaticum, Anemone narcissiflora, Salix reticulata, S. chamissonis, Equisetum arvense* L., *Carex* spp., *Festuca altaica, Artemisia arctica, Viola langsdorfii, V. biflora* L., and *Sedum roseum.*

Palmer (1945) probably included this type in his "dry tundra." Oosting (1948) noted that in northeast Greenland, important heath species were *Cassiope tetragona* and *Vaccinium uliginosum microphyllum,* that either may be dominant, that Cassiope is less important inland, and *Rhododendron lapponicum* usually occurs as patches in the dwarf shrub heath. Seidenfaden and Sørensen (1937)

noted that *Cassiope tetragona* was associated with *Vaccinium uliginosum* et al., on lower, moister parts of slopes in their ecosystem 7, "moderately moist sheltered precipices and rock ledges." Their ecosystem number 9, "moderately moist, well drained, snow patches and fossil polygon fields" was "entirely dominated by *Cassiope tetragona.*" Some additional species of common occurrence were: *Salix arctica, Polygonum viviparum* L., *Poa arctica, Hierochloe alpina, Luzula nivalis* (K. and R. P.) Trautv., *Pedicularis hirsuta* L., *Papaver radicatum* (R. P.) Trautv., and *Lycopodium selago* L., the last "exclusively associated with *Cassiope* heath." "This ecosystem is one of the few systems within the area which principally manifests itself by its vegetation, the patches and belts of brown *Cassiope* heath so conspicuous in the landscape—snow-covered in the winter, but not exposed to any considerable accumulation of snow" (p. 122). Trapnell (1933) described briefly the "open mat" type with *Cassiope tetragona* as the "physiognomic dominant" over much of the montane zone (500–600 m.) in the Godthaab Fjord region. Associated species were *Dryas integrifolia* M. Vahl., *Rhododendron lapponicum, Vaccinium uliginosum microphyllum, Diapensia lapponica* L., various herbs, a few mosses, and many lichens. This community is more xeric than the Alaskan type (number 11).

Du Rietz (1925a) wrote that *Cassiope tetragona* plays a great role in northern Lapland, greatest in the upper part of the lower alpine zone (over 1,050 m.). It may form unbroken stands over very large areas. It requires long-lasting snow-cover, in contrast to *Empetrum nigrum* heath, which occupies wind-exposed sites. The latter community, according to Du Rietz, is the most important dwarf shrub heath in the Scandinavian mountain chain. In the lower part of the lower alpine zone, *Cassiope* heath occurs in soil moderately rich in lime, but in the upper part it is indifferent to the lime content. Nordhagen (1936: 43) stated that this very characteristic community occurs on lime-rich soil in Finnmark province (where it is transitional to *Dryas* heath), but farther southwest in Troms and in neighboring parts of Finnish and Swedish Lapland, excellent stands are found on lime-poor sites. Some of the more important associated species in Nordhagen's analysis of this

TABLE V. *Alpine bearberry-mountain cranberry stand, Cape Nome, 13 miles E. of Nome. Aug. 2, 1951*

Species	1	2	3	4	5	6	7	8	9	10	Aver. Cover	Freq. %
Arctostaphylos alpina	5	4+	5	6	5	6	4+	5	5	5	4.9	100
Vaccinium vitis-idaea	3	3	4	3	4	3	4	4	3	3	3.4	100
Ledum decumbens	2	2	2	1	1+	2	1	1	1	2	1.5	100
Vaccinium uliginosum	2	2–	1		2	1	1	1		2	1.5	80
Betula nana exilis	1	2	2	1	1		2	1			1.4	70
Empetrum nigrum		1		2	1			1	2		1.4	50
Loiseleuria procumbens							1–		1–		1–	20
Salix chamissonis					1–					1–	1–	20
Hierochloe alpina		1–	1	1	1–	1	1–	1–	1–	1	1–	90
Carex lugens	1–						1–	1–	1–		1–	40
Agrostis borealis		1–	1–							1–	1–	30
Pedicularis verticillata		1–				1–			1–		1–	30
Luzula parviflora										1	—	10
Mosses	1	1	2				1	1–			1.2	50
Lichens	2	2	2	1	1	1–	3	1	1		1.6	90
No. vascular spp. per m²	6	9	7	6	8	6	8	8	8	8		
Aver. no. vasc. spp. per m²	7.4											

FIG. 7. Alpine sedge-alpine *Dryas* type at Black Hill, about 1500 feet elevation, near the head of Kougarok River, west-central Seward Peninsula. Remains of reindeer in the foreground. Alpine *Dryas* type and lichen-moss barrens on hills.

community were *Dryas octopetala, Carex rupestris* All., *Silene acaulis* L., *Polygonum viviparum, Vaccinium uliginosum, Empetrum hermaphroditum, Salix reticulata,* and *Festuca ovina* L. *Cassiope tetragona* community apparently does not occur in the Sylene and Sikilsdalen regions in central and southern Norway, because Nordhagen does not include it in his studies of these areas (1927, 1943). According to Du Rietz (1925a: 37), *Cassiope tetragona* heath is restricted to the northeastern part of the Scandinavian mountain chain.

12. *Alpine bearberry-mountain cranberry type*

A stand, about 4 inches high and a few square rods in area, of this wind-resistant community was found on gravelly material between boulders at 400 to 500 feet elevation on Cape Nome headland, east of Nome. It probably occurs in similar sites in many places in the region. An analysis is given in Table V. The chief dominants were *Arctostaphylos alpina* and *Vaccinium vitis-idaea.* Other important shrubs were *Ledum decumbens, Vaccinium uliginosum, Betula nana exilis,* and *Empetrum nigrum.* Also present were *Loiseleuria procumbens* and *Salix chamissonis.* Lichens, averaging about 0.75 inch high, formed fair cover; mosses were scattered. The average number of species per quadrat was only 7.4.

According to Oosting (1948), *Empetrum nigrum* may be a dominant locally in northeast Greenland, and where *Empetrum* is abundant, *Arctostaphylos alpina* also occurred. This type number 12 could probably be classified as a sociation in Nordhagen's association number 4 because of its resemblance to the *Arctostaphylos alpina* variant of the *Empetrum-Cetraria* sociation (1943: 95).

13. *Alpine Dryas type* (*Fig. 7*)

This type is common throughout the region on upper slopes and summits of hills and mountains. The most common and abundant species is usually *Dryas octopetala,* with a large number of associated herbs, dwarf shrubs, mosses, and lichens. On a hill, about 650 feet high, about 5 miles northeast of Nome, a total of 48 species of herbs and dwarf shrubs, and 14 species of lichens were listed by Hanson (1951: 370). A stand on a hilltop north of Egavik on the shore of Norton Sound, contained few species, similar to the stand analyzed in Table VI which was several square rods in area. Bare or lichen-covered rocks are usually dull gray in color, while the *Dryas* stands are pale bluish gray-green due to *Dryas.* Variations are caused by patches of other spe-

TABLE VI. *Alpine Dryas stand, about 13 miles east of Nome. Aug. 2, 1951*

Species	1	2	3	4	5	6	7	8	9	10	Aver. Cover	Freq. %
Dryas octopetala	3	3	6	4	6	4	4	5	5	4	4.4	100
Salix chamissonis	3	3	2		2	3		1	2	3	2.4	80
Ledum decumbens	1	1	1–	1			1–	1–	1–	1	1–	80
Empetrum nigrum							1	1	1		1	30
Rhododendron kamtschaticum		1					1	1			1	30
Loiseleuria procumbens		1		1							1	20
Diapensia lapponica obovata		1						1–			1–	20
Vaccinium vitis-idaea	3										—	10
Agrostis borealis	1–	1–		1–	1–	1–	1–		1–	1–	1–	80
Carex lugens	1–	1	1–		1–		1	1	1–	1	1–	80
Hierochloe alpina	1	1–	1	1–	1–	1–	1–				1–	70
Artemisia arctica	1–		1–		1–		1–			1–	1–	50
Luzula parviflora	1–			1				1		1	1	40
Campanula lasiocarpa	1			1–	1–						1–	30
Antennaria sp.				1							—	10
Tofieldia pusilla								1–			—	10
Mosses	1	1	1	2	2	1	2	1	1	1	1.3	100
Lichens	4	5	3	5	3	4	3	3	3	3	3.6	100
Rocks with crustose lichens	3	4	2	4	2	3	4	3	3	1	2.9	100
No. vascular spp. per m²	10	9	6	8	7	4	8	9	6	7		
Aver. no. vasc. spp. per m²	7.4											

cies, especially *Loiseleuria procumbens,* giving a greener color. Darker green areas and stripes occur in moister depression because of the greater density and more luxuriant growth of sedges, low willows, grasses, and *Cassiope tetragona,* the last often dusky green in color. The soil under rocks remains moist during the summer, but the wind blows much of the time, causing many of these areas to be bare in winter. Many kinds of lichens are scattered, but the cover and density are low and the height is usually less than 0.5–1.0 inch. In small depressions they are denser and up to 2 inches high. The variety of dwarf shrubs and herbaceous plants gives a wide choice of forage for summer grazing by reindeer seeking higher elevations to escape flies and mosquitoes. In many places, the lichens are too short and scattered for winter grazing, but when icing-over occurs at lower elevations, this type is most important because of its freedom from snow much of the time. The lichens, though short, are more nutritious than the taller kinds (Palmer 1945). A similar community on raised gravelly beaches, exposed to wind, in the vicinity of Kotzebue, was described by Hanson (1951: 369). The chief species were *Dryas integrifolia, Saxifraga tricuspidata* Retz., *Empetrum nigrum, Arctostaphylos alpina,* and *Salix reticulata.* Short lichens and mosses covered much of the ground between the shrubs.

Palmer and Rouse (1945) also called this community the alpine *Dryas* type. Oosting (1948) discussed a *Dryas*-sedge (preclimax) community on gravel areas in which many pioneer species also were present, in northeast Greenland. According to Seidenfaden and Sørensen (1937), *Dryas octopetala* is an important constituent of their dry-barren-ground and dry-loess-fields ecosystems in northeast Greenland. One of Trapnell's (1933) important communities in the Godthaab Fjord region was the *Dryas* mat barren, comprising cushions of *D. integrifolia* among lichens and xeric herbs. Nordhagen (1943) included a similar type in his *Dryas-heath* alliance, Kobresieto-Dryadion, in Order L, rock communities in mountainous regions. He stated that

this alliance included a number of associations and sociations, of which the most important were Dryadetum scandinavicum, Kobresietum myosuroides scandinavicum, and Caricetum nardinae. Floristically and environmentally, this alliance is closely related to the middle European Seslerion coeruleae alliance. Earlier, Nordhagen (1936) had described and analyzed 10 sociations in this alliance, some with few species in them, usually xerophilous and on rocks rich in lime. Additional research in the hills and mountains of western Alaska would undoubtedly reveal communities with greater similarity to those of Norway. The *Dryas-Kobresia-Hedysarum* community at 3,200 feet in Mt. McKinley National Park described by Hanson (1951) is in this alliance also, so this alliance is widely represented in Alaska. It furnishes valuable grazing for reindeer, caribou, and mountain sheep.

Christophersen (1945) stated that the *Dryas*-flora (*Dryas octopetala, Salix polaris* Wahl., *Betula nana,* and other hardy species) formed the first vegetation following the glacial period in Norway, and some of these species may have survived the glacial period in favorable spots not covered by ice. He also stated that *Dryas octopetala* grows only where there is lime in the soil, and it is found farther north than any other flowering plant, as far north as Lat. 83° 15′ in Greenland. Lagerborg and Holmboe (1937–40) wrote that this species is found only in soil containing lime, and that it forms the most characteristic kind of *Dryas*-heath, to which attention was called by Chr. Smith as early as 1812. Du Rietz (1925a) also stated that *Dryas octopetala*-heath is restricted to calcareous substrata, and that it is indifferent to the duration of snow cover. Du Rietz (1924) published an analysis of a *Dryas octopetala* heath at 2,350 meters elevation in the Alps, which resembles the Scandinavian and Alaskan communities. Besides the dominant *D. octopetala,* species common in stands of the three locations were *Polygonum viviparum, Silene acaulis,* and *Cetraria islandica.* Du Rietz reported also *Selaginella selaginoides* in a *Dryas*-heath in the Alps, Nordhagen (1936, 1943) in similar communities in Norway, and Hanson (1951) in Alaska.

IV. Dwarf Shrub-Marsh Types

This major group is distinguished from the dwarf heath shrub types on firm land by the association of such characteristic bog species as *Rubus chamaemorus, Oxycoccus microcarpus, Carex* spp., *Eriophorum* spp., *Sphagnum* spp., and mosses, with dwarf shrubs including *Betula nana exilis, Vaccinium vitis-idaea, V. uliginosum, Ledum decumbens,* and *Empetrum nigrum.* Lichens may be abundant also. This group resembles very much Nordhagen's Order J, Oxycocco-Ledetalia palustris (1943), the "Zwergstrauch Gesellschaften der Moorböden" (1936) occurring on hummocks or series of joined hummocks and mounds as "islands" and "stringers" in complex types, or surrounded by grass-marsh. According to Nordhagen, this group forms the final stage in the progressive development from open water to grass-marsh to dwarf-shrub marsh. When hummocks reach a certain height they become drier, the protecting snow-cover becomes thinner, and lichens may become dominant, as described by Hanson (1951: 338).

14. *Cloudberry-dwarf shrub marsh*

Dwarf shrub marsh types are of common occurrence on lower, flat lands in the region. In a previous publication (Hanson 1951: 338), a stand was described on low mounds and ridges surrounding fresh water marsh on the Kotzebue spit. On the lowlands north of Imuruk Basin, east of Teller, large areas are covered with the cloudberry-dwarf shrub marsh type. An area examined on August 6, 1951, had a prolific crop of berries, being picked by two camps of Eskimos for winter. As in Norway, this type shows a better development of the cloudberry than occurs in other types. Analysis of a stand, about

TABLE VII. *Cloudberry-dwarf shrub-marsh, about 12 miles east of Nome. Aug. 2, 1951*

Species	1	2	3	4	5	6	7	8	9	10	Aver. Cover	Freq. %
Vaccinium vitis-idaea	4	4	4	3	3	4	4	3+	3	3+	3.5	100
Betula nana exilis	4	3	4+	4	3	4	3	2	2	4	3.3	100
Empetrum nigrum	3	4	4	3	4	4	2	2+	2+	4	3.2	100
Rubus chamaemorus	3+	3	3	3	3−	2	2	3	3	3+	2.8	100
Ledum decumbens	2−	2		2+	2	2	3−	2+	2	3	2.2	90
Vaccinium uliginosum		1				1	2−	1	3		1.6	50
Spiraea beauverdiana		1	1	1−	1−	1	1	1			1	70
Arctostaphylos alpina								4			—	10
Cornus suecica	1−	1−	1−		1−	1	1				1−	60
Calamagrostis canadensis			1−	1	1	1−	1−	1−			1−	60
Equisetum sylvaticum			1−		1−						1−	20
Mosses	1	1	1	2	6	4	3	1	5	2	2.6	100
Lichens	3	3	2	3	3	2	3	3	5	4	3.1	100
No. vascular spp. per m²	6	8	8	7	9	9	9	9	6	5		
Aver. no. vasc. spp. per m²	7.6											

Additional species in the stand but not in any quadrat; *Salix pulchra.*

0.5 acre in area, of this type east of Nome is given in Table VII. It occurred on moist peat, in strips parallel to the gentle south-facing slope, alternating with fresh water sedge-marsh. It was only a few hundred feet from the seacoast, exposed to strong south winds. The plants were only 3 to 6 inches high, the cloudberry and dwarf heath shrubs giving it a characteristic appearance. It was conspicuous from a distance because of the large leaves, turning orange to red in late summer, and the large fruits which turn pale yellow to pink. In order of high frequency and cover, *Vaccinium vitis-idaea* rated first, followed by *Betula nana exilis, Empetrum nigrum, Rubus chamaemorus, Ledum decumbens,* and *Vaccinium uliginosum.* Both lichens and mosses rated high in cover and frequency. The average number of vascular species per quadrat was only 7.6, total number in 10 square-meter quadrats was 12.

According to Nordhagen (1943) this order was first recognized in Finland. Oosting (1948) mentioned that raised parts of older bogs in northeast Greenland show all the characteristics of typical ericaceous heath, *Rubus chamaemorus* was not listed. Trapnell (1933: 327) found in the Godthaab Fjord region a somewhat similar community, with *Vaccinium uliginosum* and *Drepanocladus* sp. forming a cover on turf hummocks, following an earlier stage of *Carex rariflora* (Wahl.) J. F. Smith-*Salix chlorocladus.*

V. HERB-DWARF SHRUB TYPES

15. *Alpine sedge-alpine Dryas type (Fig. 7)*

This type occurs at higher elevations, as, for example, at 1,500 feet on Black Hill, in the west-central part of Seward Peninsula. It grows below the alpine *Dryas* type in sites where more soil has accumulated between the rocks and where there is more moisture and probably longer lasting snow-cover. Common species in this stand were *Carex spp., Dryas octopetala, Salix reticulata, Luzula confusa* Lindeb., *Hierochloe alpina, Oxytropis* sp., *Poa arctica,* and mosses. Lichens were scattered, mostly on the sides of low hummocks, the chief species being *Thamnolia vermicularis,* and *Stereocaulon tomentosum,* with very little *Cetraria* spp. and *Cladonia* spp. The presence of *Dryas octopetala* indicated lime in the soil. A stand very similar to this was studied in 1949 on Eagle Sum-

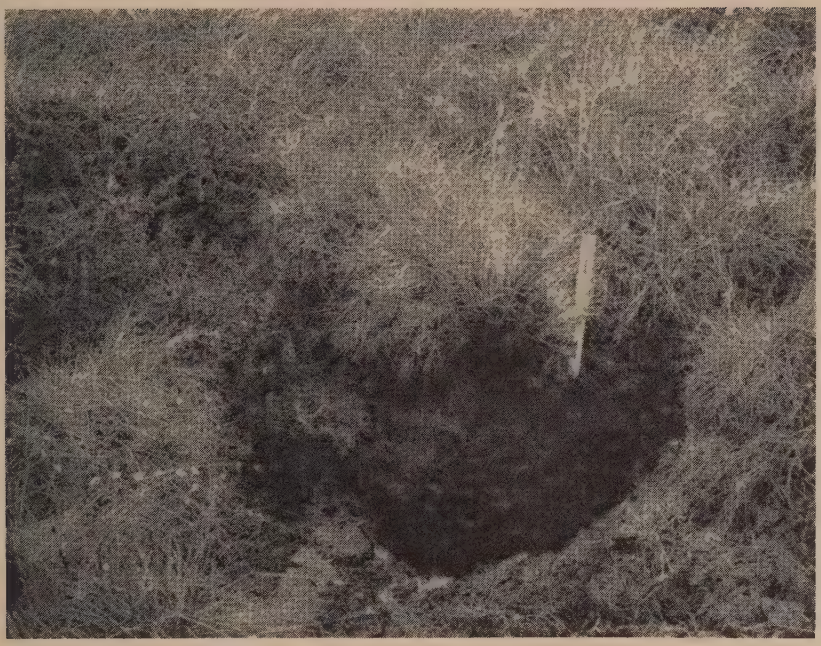

FIG. 8. Detail of the cottongrass-sedge-dwarf heath shrub complex on Baldwin Peninsula. Dwarf birch is prominent at left between the cottongrass tussocks. Aug. 12, 1951.

mit, northwest of Fairbanks, at an elevation of 3,900 feet (Hanson 1950).

This type is closely related to the alpine *Dryas* type (number 13), because of the abundance of *Dryas octopetala* and other species listed above, both belonging to the same alliance, discussed under type 13. It is placed in the herb-dwarf shrub group because of the physiognomic importance of the herbaceous species. The alpine sedge-alpine *Dryas* type corresponds most closely to Nordhagen's (1936: 37, 39) *Dryas octopetala-Carex rupestris* sociation in the *Dryas*-heath alliance. It also corresponds to Du Rietz's (1925a) *Dryas* meadows on soils rich in lime in the lower alpine region and Christophersens' (1945) *Dryas*-grass-heath communities in the middle alpine zone, both in Scandinavia.

16. *Cottongrass-sedge-dwarf heath shrub complex* (*Figs. 2, 3, 4, 6, 8*)

This is called a "complex" in recognition of the occurrence of several communities and microcommunities in close association. These communities often occupy only a few square feet, or less, but in places they form a fairly uniform cover over many acres. The frequent occurrence of mounds and hummocks, with ponds, lakes, and marshes adds to the heterogeneity in many areas. Larger stands of aquatic and sedge marsh types can readily be segregated. However, areas where the summit of a mound may be in the dwarf shrub-heath-lichens type, the depression a small sedge marsh type, and in other spots a mixture of cottongrass tussocks, scattered sedges, and dwarf shrubs, it appears best to designate the vegetation on the area as a complex.

This complex covers more area than any other type in the region. It can probably be considered the most characteristic kind of tundra in northwestern Alaska, in view of the tussock form of growth of the cottongrass (*Eriophorum spissum* Fern.), the chief tussock former. There is considerable variation, from almost continuous and uniform growth of well

developed tussocks with sparse growth of sedges and dwarf shrubs (Fig. 6), to stands where the tussocks are sparse or almost lacking and sedges and dwarf shrubs are abundant (Fig. 3). The land may be fairly level and uniform, or it may be hummocky and irregular, with small wet areas of sedge marsh in the depressions. The dwarf shrubs, especially dwarf birch, Laborador tea, crowberry, blueberry, and mountain cranberry, and in places alpine bearberry and dwarf willows, grow usually in the depressions, on the sides of tussocks, and they may dominate mounds and hummocks. Often the bottom of the spaces between the tussocks may be filled with several inches of moss or *Sphagnum*, upon which the dwarf shrubs grow. Lichens also grow on mosses and *Sphagnum* in depressions and on the sides and tops of tussocks or on the tops and sides of hummocks where they may form most of the cover, especially where they are exposed to much wind.

Usually this complex occurs on fairly level to gently sloping land, underlaid by peat, with perennially frozen ground as close as 1 to 1.5 feet below the surface in places. The tussocks can be seen from the air to a height of about 1,000 feet, giving an irregular stippled appearance, pale yellowish green in color, and, if lichens are abundant, with a pale yellowish tinge. Cottongrass areas appear bright white when headed out (Fig. 6). Lichen areas can be distinguished from the cottongrass heads by the more yellowish gray color. Hummocks often have a cover of dwarf shrubs, brownish green in color, adding heterogeneity to the stand. Interspersed sedge-marsh areas are usually bright green, willow thickets are darker green, and alder clumps are dark bluish green.

The cottongrass complex, when not overgrazed or burned, furnishes much lichen forage because the lichens find almost optimum conditions of moisture and light in the spaces between the tussocks. Often they form dense tufts, 4 to 5 inches high.

The stand shown in Fig. 8, on Baldwin Peninsula, was described in detail in an earlier paper (Hanson 1950: 625, 626). The "tussock-birch-heath vegetation" of Hopkins and Sigafoos (1951), described in much detail, especially with respect to the results of frost action, corresponds to the cottongrass-sedge-dwarf heath shrub complex. Palmer (1945) used the term "tundra" for this complex, and he divided it into the wet and dry kinds, the latter having more lichens and dwarf shrubs. Porsild (1951: 132) stated: "In unglaciated Alaska—a climax undoubtedly has been attained in the 'niggerhead' tundra which is so characteristic of the coastal plain landscape." This complex shows some resemblance to associations, especially numbers 99 and 100, in Nordhagen's "Torfmoosreiche Graskrautmoore" (1928), placed later in Alliance 17, the meso-oligotrophic grass marshes (1936: 17, 1943). The cottongrass complex in Alaska seems to be almost intermediate to Nordhagen's Order I-A, meso-oligotrophic grass marshes (Scheuchzerietalia) and Order J, dwarf shrub marsh (Oxycocco-Ledetalia palustris) because the dwarf shrubs are more abundant usually than in Order I-A, but they do not dominate as in Order J. Instead, cottongrass as tussocks usually dominate (Figs. 6, 8), but often sedges dominate (Fig. 3). While cottongrass is rooted in mineral soil (Fig. 8), shown also by Hopkins and Sigafoos (1951: 64), mosses and *Sphagnum* usually form mats and tufts between the tussocks and a layer of peat usually lies beneath them. However, the cottongrass complex does not fit Order I-A very well because there is too great an abundance and variety of dwarf shrubs, greater dominance of cottongrass, and absence or sparseness of species that usually grow in wetter areas, such as *Scirpus caespitosus* L. and *Menyanthes trifoliata* L. The cottongrass complex appears to be intermediate to the grass marshes rich in mosses, the cottongrass-*Scirpus* marsh, and the dwarf shrub marshes in the classification of marsh and

bog types in Norway by Løddesøl and Lid (1950). Closer resemblance, however, is found to the community described as "jernik" by Imanishi (1950) in northwestern Manchuria, a sedge marsh (*Carex* spp. and *Eriophorum vaginatum* L.), made up of tussocks about a foot apart, often containing *Sphagnum,* dwarf *Betula exilis,* and *B. fruticosa.*

The cottongrass-sedge-dwarf heath shrub complex, then, appears to be floristically and physiognomically a unique type, without close resemblance to communities in Scandinavia. Sociological analyses are needed for more precise comparisons. Environmental factors undoubtedly play an important role in this uniqueness.

VI. Herb Types

The types included in this class are characterized by the dominance of herbaceous plants, usually sedges or grasses. Forbs may be important in some of them, but dwarf shrubs and shrubs are usually scarce or lacking.

17. *Sedge marshes, saline and fresh water* (*Figs. 4, 5*)

Saline marshes occur extensively on estuaries, borders of lagoons, and other areas near the sea. Fresh-water marshes are also extensive, bordering lakes and streams, in drainage strips in shallow draws separating expanses of the cottongrass complex, and in other poorly drained sites (Fig. 5). The sedges vary in salt tolerance from saline species such as *Carex cryptocarpa* C. A. Mey. and *C. subspathacea* Wormskj., to fresh-water species such as *C. aquatilis* and *C. rotundata* Wahl. Other characteristic species on saline estuaries, often early invaders on mud flats, are *Puccinellia borealis* Swal., *Stellaria humifusa* Rottb., and *Potentilla pacifica* Howell. The total number of species is few in saline marshes, but often high in fresh-water marshes. Narrowleaf cottongrass (*Eriophorum angustifolium* Roth.) is often conspicuous in the latter, especially where the ground has been disturbed, as by tractors. Some additional species in fresh-water marshes are *Salix pulchra, S. richardsonii, S. reticulata, S. ovalifolia camdensis* Schneid., *Potentilla fruticosa, Andromeda polifolia, Saxifraga hirculus* L., *Dodecatheon frigidum* C. & S., *Saussurea angustifolia* DC., *Polygonum bistorta plumosum,* P. *viviparum, Arctagrostis latifolia* (R. Br.) Griseb., *Juncus triglumis* L., *Iris setosa* Pall., *Thalictrum alpinum* L., *Luzula multiflora* (Retz.) Lej., *Equisetum arvense, Eriophorum spissum, E. brachyantherum* Trautv., *Calamagrostis* spp., *Pedicularis capitata, P. arctica* R. Br., *P. oederi* Vahl., *Petasites frigidus,* and *Gentiana glauca* Pall. Mosses and *Sphagnum* form a ground layer in many places.

An analysis is given in Table VIII of a sedge marsh containing a large number of dwarf shrubs. This stand, occupying several acres, was on a moderate, south facing slope near Cape Nome. It alternated with stands of the dwarf shrub marsh type (Table VII). It is classified with the fresh-water marshes because of the dominance of the sedges, the prominence of *Petasites frigidus,* and the abundance of moss.

Often hummocks, 6 to 8 inches high, are scattered over the surface in the fresh-water marshes. They have a greater cover of grasses, especially *Calamagrostis canadensis, Festuca altaica,* and *Arctagrostis latifolia,* and dwarf shrubs, than the depressions. From the air the sedge marshes are easily recognized because of the pale green to yellow green color and the smooth texture.

A profile made on July 1, 1950, in a depression in a stand of this type about 10 miles north of Nome showed dark red to brown fibrous peat to a depth of 12 inches. Two layers of dark gray silt loam occurred at 3–4 and at 5–7 inches. Below 12 inches there was gravel and rocks and the soil was frozen. The profile was seeping with water, the reaction was pH 5.6 to 5.8. The roots were mostly in the upper 4 inches. Under a 6-inch high hummock, peat formed a layer 14 inches

TABLE VIII. *Sedge-moss marsh, about 12 miles east of Nome. Aug. 2, 1951*

Species	1	2	3	4	5	6	7	8	9	10	Aver. Cover	Freq. %
Carex bigelowii	2	4	5	4	4	4	5	4	4	3	3.9	100
Eriophorum angustifolium	5			1		1	1—			1	1.8	50
Vaccinium uliginosum	1	2	3	4	4	2	4	2	2	3	2.7	100
Empetrum nigrum	3	2—	2	3	2	3	3	3	3	2	2.6	100
Ledum decumbens	1	2—	1	2	1	2	2	2	1	2	1.6	100
Vaccinium vitis-idaea	1	1	1	2	2	1	2	2	1	2—	1.5	100
Arctostaphylos alpina		3	2		2	2			1	2	2	60
Betula nana exilis			1	1	1—	1	1—	3	3		1.6	70
Rubus chamaemorus	1—	1	1		1—	1—		3	1	2—	1.1	80
Alnus crispa	1		1—								1—	20
Salix pulchra	1—										—	10
Salix chamissonis								1			—	10
Petasites frigidus	1	3	1—		1		1				1.4	50
Luzula multiflora	1—	1—									1—	20
Pedicularis verticillata		1—									—	10
Mosses	2	3	5	5	3	4	4	4	3	3	3.6	100
Lichens	1	2	3	3	4	4	4	4	4	5	3.4	100
No. vascular spp. per m²	11	10	10	7	9	9	8	8	8	8		
Aver. no. vasc. spp. per m²	8.8											

thick on top of dark gray silt loam which continued to the frozen ground at 16 inches.

Hanson (1951) described and gave analyses of stands of *Carex subspathacea, C. rariflora,* and *C. aquatilis-C. rotundata* on the lowlands in the vicinity of Kotzebue, and discussed in detail differences in the flora and environment of hummocks and depressions. The formation of mounds and hummocks on the Kotzebue lowlands was discussed by Hanson (1950: 624) as being due to a number of processes including frost action and the accumulation of plant remains, and some of the voluminous literature was cited. Hopkins and Sigafoos (1951) and Sigafoos (1951) discussed the formation of tussocks, mounds, and hummocks, peat ridges, etc., as being caused chiefly by frost action. They described a "sedge sod" type, occurring in poorly drained sites where water occurs at the surface and where lateral movement is slow. Palmer (1945) and Palmer and Rouse (1945) included lowlands sedge marshes in their wet-tundra. Porsild (1951) included such communities in "marsh and wet tundra," and in "lagoon and salt marsh subject to floods."

Oosting (1948) presented the importance of sedge marshes in hydrarch successions in northeast Greenland, in which were included communities of *Juncus-Carex, Carex* and *Eriophorum.* Apparently similar to the *Carex rariflora* community at Kotzebue, were the "Extensive areas of saturated soil between the pools, —covered with a turf-like mat of *Carex rariflora*" (p. 255). Seidenfaden and Sørensen (1937) stated that their ecosystem "water-soaked ground-swamps" occurs in all the climatic zones and on all kinds of soil in the area included in their study in northeast Greenland. Many species are the same as in northwestern Alaska. Among the species listed in salt marshes in another ecosystem is *Carex subspathacea.* Nordhagen (1943) proposed a classification of marshes, bogs, and willow thickets with grass-marsh or bog vegetation ("myr"), under two orders in the class "Eriophoretae," with 5 alliances and 18 associations. The first order, "eutrophic-mesotrophic grass marshes (Caricetalia goodenowii)," cor-

responding to the "Wiessenmoore" or the "Flachmoore" of central Europe, comprises 3 alliances: 1) Caricion atrofuscae-saxatilis on lime-rich ground in mountains and subarctic regions, 2) Schoenion-ferrugini on lime-rich ground in lower regions, and 3) Caricion canescentis-goodenowii, broadly tolerant in soil needs, in all regions up to the midalpine. Most of the Alaskan sedge marshes studied would probably fit best in his third alliance. Nordhagen's second order, the "meso-oligotrophuc grass marshes (Scheuchzerietalia)," corresponds in part to the "Zwischenmoore" of central Europe, and the rest to the oligotrophic-acidiphilous *Sphagnum-rich* grass-marsh or bog of the marsh complex termed "hogmossar' in Sweden, together with related types. This order has two alliances: 4) Stygio-Caricion limosae on wet ground, mid-acidiphilous, meso-oligitrophic, from lowlands to highlands, and, 5) Leuko-Scheuchzerion, the most oligotrophic-acidiphilous of these five alliances, with a ground layer usually of *Sphagnum,* usually occurring below subalpine and subarctic regions. The first three of these alliances are supplied with infiltration water, ground water or from streams, occurring in depressions with a permanently high ground-water level (varying in depth with precipitation and melting time of snow).

18. *Sedge-Sphagnum-moss bog*

This type is characterized largely by the abundant growth of *Sphagnum,* often several inches thick, usually with intermixed mosses, forming the ground layer. Sedges, cottongrass, dwarf shrubs especially heaths, and a few grasses and forbs grow to a height of about 15 inches on the cushiony substratum. In the eastern part of the region under study, small black spruces (*Picea mariana* (Mill.) B. S. P.) are also found. Lichens are usually sparse. This type is widespread, found usually as small stands in depressions, and can ordinarily be recognized from the air by the bright yellowish green or orange color of *Sphagnum* and mosses, beneath the pale green of the sedges.

The most abundant species in a well developed stand occupying a depression which appeared to have been a pond, on the north side of Salmon Lake, about 30 miles north of Nome, were *Carex* spp., *Sphagnum* spp., and *Rubus chamaemorus.* Fairly numerous were *Eriophorum* sp., *Betula nana exilis, Vaccinium vitis-idaea,* and *Ledum decumbens.* The following were infrequent to scarce; *Vaccinium uliginosum, Empetrum nigrum, Oxycoccus microcarpus,* mosses, lichens especially *Cetraria islandica,* and *Salix* sp.

Sedge-*Sphagnum*-moss bogs, with more or less dwarf shrubs, are widely distributed in the northern hemisphere (Hanson 1951: 367). Dachnowski-Stokes (1941) described the vegetation, and especially the profiles of many bogs in Alaska. When sedges are dominant many of the Alaskan stands can probably be classified under Nordhagen's 5th alliance, Leuko-Scheuchzerion, in the meso-oligotrophic grass-marsh order (see discussion under type number 17).

19. *Grassland types*

The most common grassland type is the bluejoint community (*Calamagrostis canadensis*). It occurs in various sites such as mounds and hummocks in fresh water sedge marshes, on fairly well drained knolls and slopes, on disturbed ground around buildings, mines, roadsides, corrals, in places where the snow lies late, etc. The perennial frost is usually near the surface. From the air, this type appears pale yellow to yellowish green due to the old foliage forming a loose mat on the ground until the new foliage becomes tall enough to give it a pale green color. Later in the season it appears pale purple because of the flowers. Descriptions of specific stands were published by Hanson (1951: 349).

Tall fescue (*Festuca altaica*) stands were seen occasionally occupying small areas on steep south-facing slopes along creeks. Dense stands resembled some-

what the preceding in appearance, but open stands were more tufted, and contained more dwarf heath shrub and lichens. The deep soil is rich in organic matter. A more detailed description was given by the writer in a previous paper (1951: 353).

Mixtures of bluejoint and tall fescue with sedges, dwarf shrubs, and with *Arctagrostis latifolia* (R. Br.) Griseb. were found on banks of streams, in valley bottoms, and between willow thickets on slopes, but usually the areas occupied were small. One stand of this kind, located about 10 miles northeast of Nome on a gentle east-facing slope, was studied in detail. The willows surrounding it were 2.5 to 4 feet tall. Abundant species were *Carex* sp., *Solidago virgaurea* L., *Salix reticulata,* mosses, and *Arctagrostis latifolia.* Moderately abundant were *Potentilla fruticosa, Vaccinium uliginosum,* and *Festuca altaica.* The following were infrequent to scarce: *Cerastium beeringianum* C. & S., *Petasites frigidus, Mertensia paniculata, Arctostaphylos alpina, Empetrum nigrum, Botrychium lunaria* (L.) Sw., *Vaccinium vitis-idaea, Alopecurus alpinus* L., and lichens on some of the hummocks. On the surface was an inch-layer of moss, liverworts, and litter. The soil in the first 4.5 inches below the litter was dark reddish brown, mostly organic matter but with a little silt, moist, with very many roots and rhizomes. Between 4.5 and 12.5 inches was brown silt, with occasional pockets of reddish brown silt rich in organic matter, wet, with numerous roots. Between 12.5 and 22.5 inches was olive gray to yellow brown silt with schistose rocks and gravel, wet, rather impervious to water, compact, the rocks becoming more numerous with depth. The roots decreased rapidly in number in this horizon, working depth was at 20 inches.

Other grass species such as bluegrasses and alpine holy grass (*Hierochloe alpina*), in association with sedges and many species of forbs form extensive communities of higher elevations and in late snow-melting sites. Along sandy and gravelly beaches, above the reach of ordinary high tides, and along some streams, is found the distinctive beach rye type (*Elymus mollis* Trin.) growing to about 5 feet in height. This type is widespread in Alaska and other northern lands (Hanson 1951). Associated with this coarse grass is usually the beach pea (*Lathyrus maritimus* (L.) Bigel.), *Poa eminens* Presl., and a few other forbs. First invaders on these shores are the mat-like sea lungwort (*Mertensia maritima* (L.) G. Don.) and sea-beach sandwort (*Arenaria peploides* L.). On the landward side in more stabilized soil, *Festuca rubra* L. with *Poa* sp., and a variety of forbs often forms a meadow-like community. Lichens are absent from these beach types. The beach rye type is conspicuous from the air, appearing pale bluish in color. It is important in binding sand and gravel, offering much resistance to erosion by waves and wind. Porsild (1951) included similar vegetation in "sand dunes and gravel beaches" in "strand communities group."

20. *Aquatic types* (*Fig. 4*)

In shallow parts of fresh-water ponds and in the bordering wet soil of ponds and streams occur species such as *Ranunculus pallasii* Schlecht., *R. aquatilis* L., *Hippuris vulgaris* L., *Potamogeton* spp., *Callitriche* sp., *Equisetum fluviatile* L., *Carex aquatilis,* and others. In brackish water *C. subspathacea* and *Hippuris* sp. also occur. Porsild (1951) separated his group "vegetation of fresh waters" into a) "ponds and lakes," and b) "brooks and rivers."

21. *Lichen-moss barrens* (*Figs. 5, 7*)

The alpine *Dryas* type persists in many favorable areas at higher elevations in the mountains, but as the soil becomes thinner and other environmental conditions less suitable, the vegetation becomes reduced to mostly crustose and foliose lichens, mosses, and very short herbs and dwarf shrubs in depressions and in other

protected spots, and finally the rocks become almost bare. Porsild (1951) included this type in his "rock desert" community.

22. *Ruderal types*

These weed or weed-like types occur on ground that has been more or less disturbed, as in and adjacent to towns, around mining and fishing camps, corrals, etc. *Calamagrostis canadensis* is one of the most common indicators of disturbance, but a number of annual and perennial weeds also occur such as *Epilobium angustifolium, Artemisia* spp., *et al.* This type is considered to form a group, distinct from the grassland types, because forbs often dominate.

Summary and Conclusions

1. As a result of study during the summers of 1949, 1950, and 1951, a preliminary classification of the vegetation of northwestern Alaska is presented. It contains 6 major physiognomic classes and 22 types.

2. A characterization is given of each type, including the species composition, some of the environmental conditions, and aerial recognition characteristics.

3. Eight new phytosociological analyses of different communities are presented in tables.

4. The types occupying the largest land areas are the cottongrass-sedge-dwarf shrub-heath complex, sedge marshes, alpine *Dryas,* dwarf shrub, willow shrub, birch shrub, and white spruce-shrubs.

5. Important factors influencing the development and the maintenance or changes in the species composition within types are soil moisture, mineral and organic composition of the soil, soil texture, soil reaction, depth to which the soil thaws during the summer, freezing and thawing processes in the soil (congeliturbation), drainage conditions, depth and duration of snow cover, exposure to wind, biotic influences such as grazing and trampling by reindeer and other animals, rodent activities, plant competition, and various man-caused influences such as burning, drainage, flooding, earth-moving, etc.

6. Similarities of the Alaskan communities to those in other arctic and subarctic regions, especially Scandinavia, are pointed out.

7. Suitable conditions for good growth of lichens, furnishing winter pasturage for reindeer, occur in many of these type, particularly in open forest types, open stands of the birch shrub type, the dwarf birch-heath-lichens type, the blueberry-heath-lichens type, and the cottongrass-sedge-dwarf shrub heath complex. The lichens have, however, been depleted over large areas by overgrazing and fire.

8. This classification has been found useful in making aerial surveys of lichen range suitable for grazing during the winter by reindeer. The various types are valuable in indicating soil conditions such as depth to perennial frost, kind of surface and subsurface materials, and moisture and drainage conditions. As a result, the classification is of value when surveys are made for locating roadways, camp sites, landing fields, etc.

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FIELD OBSERVATIONS ON THE HABITS OF *AEDES TAENIORHYNCHUS*

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THE STUDY AREA

The east or Atlantic coast of Florida is paralleled by a chain of narrow islands which are often referred to as the Beach. In the vicinity of Fort Pierce, the lagoon separating this offshore bar from the mainland is called Indian River (Fig. 1). The outer or ocean beach is very straight and is backed by dunes behind which a number of plant associations parallel the coast. These increase in height as they succeed one another westward, from grass and weeds, through palmetto scrub, to the coastal hammock, a dense forest dominated by oaks and Sabal palms (for details, see Kurz 1942, and Davis 1943). The Indian River shore is a confusion of islands, peninsulas, coves, and sounds, more or less inundated by tide and covered with mangrove and salt marshes. These are the typical breeding areas for salt-marsh mosquitoes, and a considerable amount of control ditching was done here in the past. In the Fort Pierce region, both of Florida's salt-marsh *Aedes* occur, but during the observation period under discussion, *Aedes taeniorhynchus* (Wiedeman) predominated while *Aedes sollicitans* (Walker) was present in negligible numbers only.

We made our studies on the property of Mr. P. McConville, some six kilometers (4 mi.) north of Fort Pierce on the offshore bar. Most of the observations were made along a narrow winding road traversing this property from highway A1A near the outer beach to the Indian River shore (Fig. 1). This road crosses a number of the typical plant associations. In the first hundred meters from the highway, it cuts across palmetto scrub with *Serenoa, Coccolobis, Lantana,* and other shrubs. It then curves WNW and passes through a hammock zone with a denser vegetation of oaks and palms. In this stretch the road crosses three old ditches which have become series of pools. Some of these pools hold water fairly continuously, but most of them, as well as the road tracks which bisect them, are flooded for short periods only after rains. These ditches are lined with mangrove and with *Batis maritima, Borrichia frutescens,* and *Salicornia* sp.

Beyond the ditches, the vegetation along the road becomes more open, with many isolated shrubs separated by grass and such weeds as *Chamaecrista.* Several kinds of vines mantle this vegetation. The road then turns SSW and in a number of short turns passes through an old orchard, mostly of mango and guava, with several rare imported trees and bushes. This orchard has grown wild for ten years and is now a dense scrub.

The road ends at the Meadow (Fig. 2), a triangular open area of about half an hectare (1 acre). It is mostly covered with a *Paspalum* turf and patches of young (1–2 m. high) mangrove along the several small pools and ditches. The meadow is bordered with high Guinea grass, and in the immediate surroundings are several unusual large palms, oaks, and strangler figs. Groundsel-bush (*Baccharis halimifolia*), a 2–3 m. high shrub belonging to the composite family, is found at many places along the road and is especially common on the edge of the meadow.

SUMMARY OF LIFE HISTORY

Numerous persons working on the control of this species as well as some outstanding biologists have accumulated a considerable knowledge of its life history. Unfortunately, however, very little of this has ever been published. According to Smith (1904; republished by Headlee

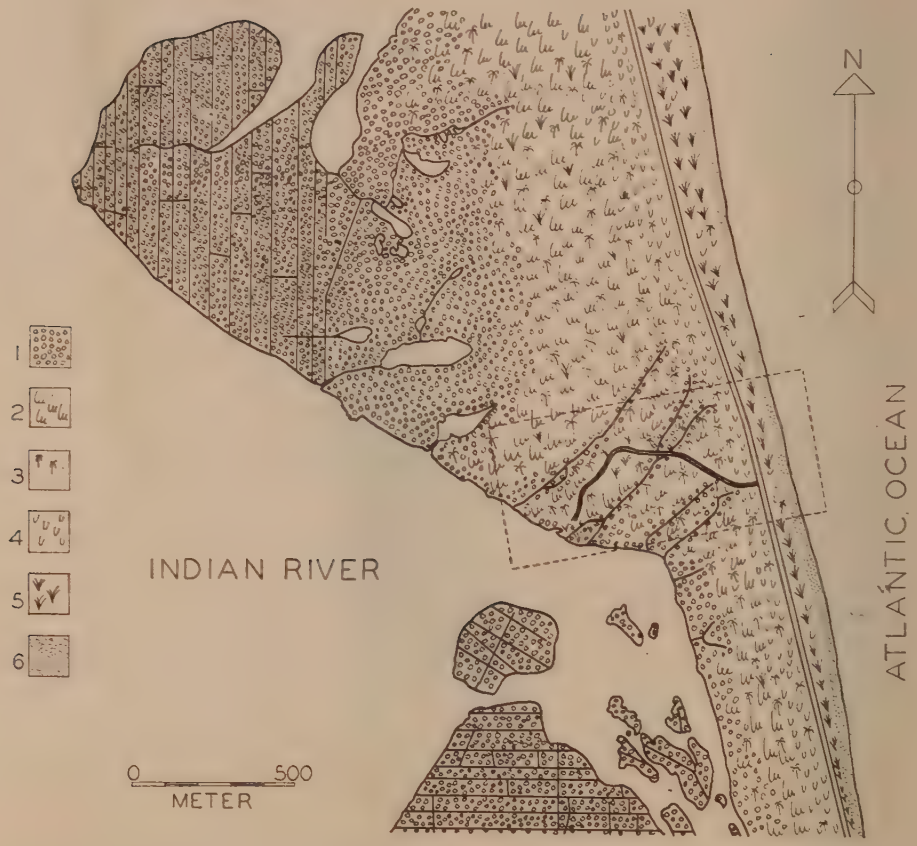

FIG. 1. Sketch map of a part of the offshore bar north of Fort Pierce. The study area is within the frame. 1, Mangrove; 2, Hammock; 3, Palms; 4, Palmetto scrub; 5, Grass and weeds; 6, Dunes.

1945), King, Bradley, and McNeel (1942); and Provost (1951), the outline of the biology of *Aedes taeniorhynchus* is as follows:

The females deposit their eggs on dry ground where they will hatch when inundated by rain or tide water. The larval development may occur in any salinity from completely fresh to ocean water. Imagines have been found far inland, but with rare exceptions, breeding is known to take place only in a narrow region along the coast.

The females are less inclined to bite in bright sunshine than the closely related *Aedes sollicitans*. The great numbers caught in light traps show that at least in some periods the females are attracted to light. They are generally believed to have migratory habits and to be able to fly long distances. The published evidence for this is not convincing; but the Florida State Board of Health has flight-range experiments in progress, the results of which will be published later by Maurice W. Provost.

NUMBER OF BROODS OBSERVED IN 1951

In our study area, egg-hatching depended solely on rain. Average precipitation in this region would be 60 to 70 mm. (2.4 to 2.8 in.) for the winter months

(November to April), and twice as much for the summer months. Nearly all the rain falls as thundershowers and is, therefore, very erratic. There is also a considerable variation from year to year. In 1951, April had three times the normal precipitation, May was a little drier than usual, and June and July had less than half the normal rainfall.

Regular observations were not started in the area until April, but occasional inspections showed that the heavy rain of February 5–6 hatched a brood which reached the late fourth instar or pupal stage on February 17. There was probably no rainfall in March sufficient to produce a new brood. The rapidly decreasing number of old females present in the study area in the first part of April very likely represented the last individuals from the February emergence (Brood I).

The next heavy rain fell on April 6–7. We had no rain gauge on the McConville property at that time, but in Fort Pierce the rainfall for these two days was recorded as 82.8 and 30.0 mm., respectively. Although the U. S. Weather Bureau station is 13 kilometers (8 mi.) away, the downpour on the study area was at least enough to fill all pools and hatch out Brood II which emerged April 16–19.

New heavy rains occurred on April 18–19: 73 mm. fell in Fort Pierce and probably more in the study area. No new brood appeared after the rain, which was the last precipitation of any importance for more than a month. On May 24–27, there fell 70 mm. of rain, and Brood III was hatched. It developed in a period without rain, and most of the waters dried up before emergence. Only two of 15 pools under observation produced imagines; the number of individuals in this brood was very small.

We do not know the origin of Brood IV. The imagines which appeared suddenly on June 21 had probably hatched as larvae on June 8–10. On June 10, 5.8 mm. of rain fell on the study area—too little to hatch larvae; but on the same day, the rainfall in Fort Pierce was 31 mm., and a private rain gauge in a grove west

FIG. 2. The Meadow.

of Fort Pierce recorded 54 mm. Since we have no record of unusually high tides at that time, it is most likely that Brood IV immigrated into the area from breeding grounds which had received sufficient rain on June 10.

June 16–18, sufficient rain fell on the study area to hatch a new brood (V), but none of the larvae survived the subsequent dry period. Broods VI and VII appeared as imagines in the area on July 9 and July 13. Their origin was unknown, but in the last week of June—when they presumably hatched—many erratic thunderstorms occurred in the vicinity of Fort Pierce, though none of importance fell on the study area.

Two more broods (VIII and IX) hatched on July 1 and July 7, respectively, but neither of them produced imagines because of the pools drying out. No further broods were observed before the discontinuation of regular observations in early August.

The Developmental Stages

Duration. Eggs seem to hatch very soon after a rain, and some of the larvae reach the second instar within 24 hours. Unpublished data given us by experienced observers indicate a total aquatic period (hatch to emergence) of 5 to 7 days. Our own observations in the Fort Pierce area, however, showed a much longer period, *viz.*, 12 to 15 days for Brood I in February, 9 to 12 and 9 to 11 days for Brood II and Brood III in mid-April and late May, respectively.

Because of drying breeding waters, most of Brood IX died in a few days, the exception being larvae in one of the ditch pools which remained wet. These larvae, hatched July 7, reached the fourth instar July 12–13, but did not develop further. On July 19, there was very little water left in the pool, and on July 23 in the morning, only a few cupfuls. It may have dried completely for a short period that day before 7.6 mm. of rain fell in the late afternoon. The next morning there was more water but fewer larvae. On July 25, the pool dried out completely, possibly for 10–12 hours. There was a rainfall of 5.6 mm. in the evening, but there were no larvae the next morning. These animals had thus stayed in the larval stage for 19 days. We cannot advance any justified explanation of this retardation of development, but we want to emphasize how propitious such a delay is in the growth of an insect which always is endangered by the drying out of the breeding water.

It is not known how long a larva can survive after the water has dried out. As long as there is a moist layer on the surface, the larva may be able to live for a considerable time; death would eventually come from lack of food rather than from respiratory difficulties. Should the surface layer become so dry that the water vapor in the air around the larva no longer is saturated, it will soon perish by desiccation. On the meadow, we observed that large larvae in the fourth instar sometimes appeared among the newly hatched larvae when the pools again were filled with rain water after having been dry for several days. They had probably survived in the holes made by the numerous crabs present on the meadow.

Smith (Headlee 1945, p. 52) found that larvae of *A. sollicitans* will survive a few hours in soft mud, but pupae under similar conditions will survive 24 hours and develop into adults. We are able to confirm this information for *A. taeniorhynchus.*

Behavior. Larvae in the first instar, and to some extent also in the second instar, spent most of the time close to the bottom and only very rarely came to the surface of the water to breathe. The relatively large surface area of the smaller larvae and the thinner cuticle seemed to permit a sufficient intake of oxygen by cuticular respiration. The older larvae came to the surface of the water as is normal for mosquito larvae.

A very peculiar habit of the larvae of *A. taeniorhynchus* is their tendency to congregate at certain places in the pools.

Larvae of such species as *Aedes cantans* (Meigen), *Aedes communis* (DeGeer), and *Theobaldia morsitans* (Theobald), previously observed by the authors in Denmark, are more or less evenly distributed in the temporary pools in which they breed. There may sometimes be more in the part of the water exposed to the sun and less where the shadow of a tree hits the surface; but generally they are so evenly distributed that a few counts of larvae seen over a standard area (a white plate of suitable size) can give a fairly good estimate of the number of mosquito larvae in a pool (Nielsen and Greve 1950, p. 228). This may occasionally be the case with *A. taeniorhynchus*, but normally the larvae are clustered together at a certain spot or at a few spots while there are few or none elsewhere in the pool. If one looks at the surface of the water at such an angle that the sky is reflected, the site of a cluster will be seen as a wrinkled spot because the larvae penetrate the surface with their siphons and spoil the reflection. In pools with dark water, it is sometimes the easiest way to locate the sites of clusters.

The small road-track pools, rarely more than 10–25 cm. wide and 2–3 m. long, seldom held more than one cluster. The cluster site could be anywhere in the pool, and could be at one place one day and another the next day. No relation to sun or shade or depth of water could be found. In the ditch pools which were larger, 1 to 1½ m. wide and 2 to 4 m. long, there were two or three congregations, and they usually remained at the same site all the time. Where the road crossed a ditch, it might be covered for 5 or 10 m. by rain water, thus forming one large pool sometimes extending into the bordering vegetation (*Batis* and *Salicornia*). The tendency to gregariousness could here take several forms. Many of the larvae were always in the vegetation, but others crowded in the open water. Sometimes the latter congregated along the border of the vegetation, thus fusing those inside and outside the plant belt. At other times the larvae in the open water crowded in the opposite parts of the pool, following the borderline between water and dry ground, in which case the outline of the pool appeared to be partly traced with a broad black line. At still other times, the larvae clustered in odd places in deeper water.

In all the pools, but especially in the big road pool, we observed at certain times the ultimate stage of the clustering habit, the so-called balling up. To our knowledge this phenomenon has not been described in print, although it is well-known to all who have worked with this species in Florida. In such a ball, the individuals are clustered so close together that it looks like a solid mass when seen from some distance although the larvae actually are swimming around very fast—apparently moving faster than normally, though this could be merely an illusion. The size of the ball depends, of course, on the number of larvae. When there are few, the ball is shaped like a more or less circular disc some 10–15 cm. in diameter; in such cases, the phenomenon is distinguished from the usual cluster by the whirling movements of the larvae and the circular outline of the congregation. In larger balls, it is especially the vertical axis which becomes longer, and the shape of the cluster changes from that of a disc to that of a spheroid. Most of the balls in the study area had a spherical form with a diameter of 10–15 cm. The balls can be considerably larger; experienced observers have told us about clusters with a vertical axis of half a meter and a diameter of 20–25 cm.

We have found that larvae react to three different stimuli: changes of light (both a shadow by day and a flashlight by night), movement of the water, and sound. The reaction is especially easy to see in balled-up larvae, which hastily scatter out in the water. Pupae may also ball up, but if adults are emerging from such a ball, there is no reaction to light.

One of the conditions for the formation of a ball is, of course, that many larvae be

present; on the other hand, even in the case of very heavy breeding, balls are not always formed. It is at present not possible to explain the habits of clustering and balling up nor to indicate under what conditions they are released.

Predators. Not only do the larvae of *A. taeniorhynchus* always live under the menace of being desiccated, but a number of predators also contribute to their decimation, chiefly minnows, water beetles, and predatory mosquitoes.

We found that in pools with minnows, no adult mosquito ever had a chance to emerge. Even if a rather large brood had hatched out, the larvae were all eaten up mostly in the first and second instar. We have never in this area seen a fourth instar larva in a pool infested with minnows.

As to the water beetles, it was noticed that larval beetles were remarkably numerous in the road-track pools while Brood III was developing. Two weeks later came the next local brood (V), and this interval seems to have corresponded to the duration of the pupal stage of the beetles because we then found adult beetles present in astonishing numbers. Even in very small pools, it was impossible to count the numbers coming to the surface for air; the water seemed to be boiling with them. They were found only in the pools in the road tracks, never in the ditch pools shaded by mangrove. They congregated in a few of the small open pools at a time, and when they had exterminated all the mosquito larvae there, they moved to the next pool. Soon after, however, the waters dried out on the road, and the beetles disappeared, although there were still plenty of mosquito larvae in the ditch pools.

Dr. Frank N. Young, of Indiana University (Bloomington, Indiana), was kind enough to identify the beetles for us. The most abundant species was *Tropistérnus lateralis nimbatus* (Say). This is a hydrophilid and is, therefore, supposed to be a plant eater as imago. The larvae are known as destroyers of anopheline larvae. Of about 130 specimens submitted, more than one hundred were *Tropisternus.* There was a single *Berosus infuscatus* LeC., another hydrophilid. Dytiscidae were represented by 16 *Thermonectus basillaris* Harris, 6 *Laccophilus proximus* Say, 2 *Copelatus chevrolati* Aube, and 1 *C. caelatipennis* Aube.

The predatory mosquito larvae were the big *Psorophora.* We did not identify the larvae, but imagines caught on the same spot were *P. ciliata* (Fabricius). Unlike the water beetles, they were found only in the shaded pools under mangrove. They were not numerous enough to have been of much importance to the *Aedes* population.

Emergence of Imagines

The males of culicines generally emerge before the females. With *Aedes taeniorhynchus,* nevertheless, we found no evidence of this, so that the difference at least was very small. It will not be considered in the following.

The emergence from a single pool lasted 2–4 days or longer, but the majority of the imagines appeared within a short period, usually on the second day of the brood emergence. The same brood might vary somewhat among different pools, probably according to temperature. The road pools directly exposed to the sun and with water temperatures of 40–41° C. (104–106° F.) in the afternoon produced imagines one or two days earlier than the shaded pools in the mangrove which were only 10–15 m. away.

Behavior. When a mosquito had come free of the pupal skin, it rested for a little while on the skin or on the surface film of the water. Now and then it moved its wings and after a few minutes was able to move over the surface without taking to the air. The movements were mainly directed by the wind, and the mosquito came ashore on the side of the pool toward which the wind was blowing. It stayed there some time, in the vegetation. There was very little spontaneous activity in this stage.

During a large emergence, the vegetation around a pool teemed with imagines. Even with a moderate wind, none would be found on the shore from which the wind was blowing, while on the opposite side of the water, they occurred at times up to ten meters downwind. When left undisturbed, very few could be seen; but clouds of mosquitoes rose in the air when they were approached within a meter or so. The flight was very weak, generally with the wind, and would rarely carry the animal more than a half to one meter away.

During the day the number of mosquitoes in the vegetation increased, and we never saw any appreciable number leave the resting places until late in the afternoon. During the last 15–30 minutes before sunset, there was an increase in activity, although it was not very spectacular. The number of individuals in the vegetation decreased slowly, but it was very difficult to see the actual flying away. After sunset when it was so dark that it was possible to see the mosquitoes only against the clear western sky, it was observed that many of them flew up into the top foliage of the mangrove and rested there. It is possible, or even likely, that many more came to rest in the tops of higher trees and palms, but it was not possible to see them. In this stage the animals had a very pronounced avoidance reaction to light so that a flashlight could not be used.

During the night only a few mosquitoes lingered close to the ground around the breeding areas. With the returning daylight, more and more were seen in the low vegetation, and at sunrise it was again possible to stir up clouds of mosquitoes at the same places as before sunset. Our observations do not permit us to decide whether these mosquitoes were the same ones that rested in the tree tops at night or new individuals which had emerged during the night.

After the mosquitoes had stayed some time, probably 12–24 hours after emergence, around the breeding site, they simply seemed to vanish. While observing Brood II, we were amazed at this disappearance shortly after emergence, and we decided, therefore, to try marking the individuals in the next brood to get more information on this point.

Marking experiments. Weathersbee and Hasell (1938) have reported successful staining of adult *Anopheles* by adding various colors to the water in which the larvae were reared. With Giemsa's solution and methylene blue, all emerging imagines were dyed although the stronger solutions seemed rather toxic. In order to see if this method could be used with culicines, a series of experiments were made with larvae of *Aedes aegypti* (Linnaeus). The laboratory of the U. S. Bureau of Entomology and Plant Quarantine in Orlando, Florida, kindly supplied eggs from their breeding stock.

Each solution was tried on ten individuals. The larvae were kept in the solution from early fourth instar until they emerged as imagines. Each group was kept in 100 ml. of the fluid in 85 mm. diameter liquid-tight paper containers of the type used for ice cream. The larvae were fed ground dog biscuit.

Methylene blue was tried in 1 : 40 and 1 : 400 of a saturated solution in water. The former was so dark that larvae in it were invisible; they all died. Of the ten larvae in the 1 : 400 solution, seven emerged after 90–145 hours, two larvae died, and the last one was killed after having been in the solution for more than 200 hours without pupating.

Giemsa's solution (a mixture of eosin and methylenazur in glycerinmethylalcohol) was tried as 1 : 100 and 1 : 200 of a commercial stock solution. It was just possible to see the larvae in the stronger solution when first made, but it eventually became much paler. All ten mosquitoes emerged from this solution after 160–180 hours, and after the same length of time, nine out of the ten emerged from the weaker solution. The last individual remained pupa for several days and was finally killed.

Methyl violet was used in 1:100, 1:200, and 1:500 of a saturated alcoholic solution. It was impossible to see the larvae in the first solution, in the second they could be discerned only with difficulty. All larvae died from these two solutions, but nine emerged from the 1:500 solution.

A few of the mosquitoes were found drowned in the jars. The majority of them were examined immediately after they were killed. None of them showed any staining of any organ examined by dissection. Thus it seemed impossible to stain culicines by this method.

We then tried the method used by Clarke (1937): dusting the mosquitoes with a mixture of aniline dyes and wheat flour. A preliminary experiment was carried out by dusting samples of 10–15 adult *A. taeniorhynchus* encaged in a lamp glass closed with wire cloth at both ends. They were then killed and examined at 10× magnification under a binocular microscope against a white background by soaking the individual in a drop of a solvent (alcohol, glycerin, chloroform, 3:2:1). In a few seconds the color, if present, appeared but would soon be difficult to see because of over-dilution in the solvent. The procedure must, therefore, be watched carefully. Eosin, methyl violet, and victoria green mixed with 3–4 parts of flour were tried; and all the mosquitoes were found to be well marked.

The actual markings in the field took place during the emergence of Brood III in the first days of June. The dusting was done with a Root hand duster kindly loaned to us by Dr. Herbert Spencer. It took place at 1800, about half an hour before the mosquitoes started to leave the resting places in the low vegetation.

On June 3, there was emergence from the big road pool referred to above. Somewhat less than one pound of mixture was used in the duster which was hardly enough to cover the area in question; and, still worse, it was found that the duster did not discharge such a small quantity of dust uniformly, resulting in many mosquitoes being blown away by the air stream without being hit by the dust. This may have been one reason why we did not find any green-colored mosquitoes the following days.

The next day (June 4), the road pool was dry; but there were clouds of mosquitoes around the ditch pools in the mangrove, and we dusted this area thoroughly with methyl violet. There was so much dye present everywhere that catching a sample then would have been purposeless; but the next day, before a new dusting took place, 59 females and 35 males were captured and 14 females and 11 males proved to have been marked. The third dusting (June 5) was again made around the ditch pools; unfortunately, we had not yet obtained a third color in sufficient quantity, so we again used methyl violet. The following day, 2 out of 9 males and 6 out of 41 females caught were colored. On June 7, only one female out of 47 caught was colored; that day only one male was captured (unmarked). Of 458 females caught the following three evenings around the dusting place, none were colored. From June 10 to June 20, 684 mosquitoes were caught on the Meadow, about 400 m. (¼ mile) from the ditch pools, and only one colored female was found (June 11). Incidentally, one sand fly (*Culicoides* sp.) marked by methyl violet happened to be in the June 11 sample from the Meadow.

Although not too much can be concluded from a single experiment carried out on a far too modest scale, there was confirmed very well the impression we had received from direct observation, *viz.*, that during the first few days of the adult life of *Aedes taeniorhynchus,* there occurs a thorough dispersal. Smith (Headlee 1945) had observed that all migrating *Aedes sollicitans* were "sterile." The same paper mentions (p. 37) that, unlike other migratory species, *Aedes cantator* (Coquillett) occasionally migrated with developed ovaries. "Sterile," therefore, probably meant with not yet mature

ovaries. In this case, our observations corroborate the view point of Smith: that the females disperse or at least start dispersal flights very early in the adult life.

Such dispersal flights would, of course, explain the disappearance of the marked individuals from the marking site. But they would not explain why, in the days immediately after the emergence, very few mosquitoes were seen. Emergence had presumably taken place from hundreds of rainpools unknown to us all along the coast; and even though the flight of each single mosquito be a migration away from the breeding site, the total sum of the flights of the newly-emerged individuals should be expected to result in a mere intermingling so that there would be everywhere a definite increase in the population. Three or four days later such an increase was very easily recognized; but immediately after the resting period following the emergence, the animals seemed simply to vanish. This was especially conspicuous during the emergence of Broods II and III when there were only a few older mosquitoes present in the study area.

In April, from the 16th to the 18th, newly-emerged individuals streamed out from the pools, rested there 12–24 hours—and disappeared. On April 19, there were far fewer around the breeding waters; on April 20 in the evening, clouds of biting females and swarming males appeared everywhere. Brood III emerged June 3, 4, and 5. On June 6, all road pools had been dry for two days, and only a few stragglers emerged from the ditch pools; mosquitoes were nowhere more numerous than they had been on June 2 except at one place (at the "knee" on the road, halfway between the ditch pools and the Meadow) where a few males swarmed a few minutes. It was not until the next evening that new females started to bite and attacked in large numbers. Simultaneously, the males started swarming everywhere.

We are so far unable to report further information on this apparent disappearance of the mosquitoes. It demonstrates, however, how well hidden these animals are during periods of rest. We shall give more examples, but want here to point out that when they are not doing anything spectacular, such as biting or swarming, they are hidden in such well-protected resting places that they are completely lost to view.

Habits of the Females

Flights of egg-filled females. It has already been mentioned that the females start biting four days after the first emergence. This first biting charge of a new brood is rather conspicuous and annoying. For Brood III it lasted two days, June 7 and June 8, while there were astonishingly few mosquitoes the following two days. On the last of these days, June 10, conditions seemed especially ideal for biting: 6 mm. of rain had fallen in the afternoon, the humidity was high, and the wind slight. It was a pleasant surprise to be able to make observations of male swarms at dusk with hardly any annoyance from biting females.

On this latter evening three-quarters of an hour after sunset, at 2000, when it was quite dark, we found, however, that there were clouds of mosquitoes swarming around the road pools and ditch pools. At first we believed it to be another species of much lighter color, but a closer examination showed that they were female *Aedes taeniorhynchus* with the abdomen so distended by eggs that the pale intersegmental parts of the skin gave them a peculiar light appearance. They were flying around one another in a cloud from the ground up to a height of 7–8 m. Most of them flew over the road and the ditches, and there were none over the drier parts outside the breeding areas. The flight of the individual mosquito was slow and without sudden changes in direction, graceful but with the same majestic calm which is seen in a female which has just finished a blood meal, and which in both cases is probably caused by the heavy weight of the abdomen.

The behavior of these females contrasted

sharply to the normal in two ways: hardly any of these thousands and thousands of females tried to bite us, and they were not repelled by light. On the contrary, small clouds of some 20–30 individuals in front of the truck headlamps seemed to indicate at least some attraction to light. Both the biting and the newly-emerged females are repelled by light. Smith (Headlee 1945, p. 54) had observed that "late in the season" "mostly gravid examples" of a number of species, among which is included *Aedes taeniorhynchus,* are attracted to electric light.

We saw many of these females floating down to the grass and other low places near the ground, especially close to the water surface (there was water in the tracks that evening); but although we were able to examine them at very close range and with plenty of light, we did not see any of them laying eggs. In some cases they flew up again after a short rest, in others they stayed until we left. When at rest they first moved their hind legs a great deal, but this movement eventually became slower and at intervals ceased completely; it looked as if they were falling asleep. After about half an hour, more and more females came to rest, and the number of flying females had decreased very much.

The same phenomenon was observed again the next evening (June 11), but the number of individuals was much smaller. On June 12, there were many biting females; no egg-laying female was seen on any of the subsequent nights until June 15 when there were a few and on June 16 when there were some more. Flights of females with eggs were again observed on June 21 and 22, but only with very few individuals. The biting intensity is dependent on factors, many of which are so far unknown to us; but during this period, there was a very marked decrease in the number attacking us. There were few during June 15–16 when the females with eggs were flying, but more June 17–18 which were the last days in this period when the biting was annoying.

As far as we know, there have never been described any special flight habits of egg-laying culicines. For anophelines, several observers have described a special flight during the egg-laying, *e.g.,* Kennedy (Bates 1949, p. 94–95), and Russell and Rao (1942). These descriptions conform very closely with our observations, especially with regard to the hovering flight without sharp turns.

Flights of egg-filled females were again observed twice in July, but neither of these was as spectacular as the first one.

Longevity. The decrease in biting activity referred to above suggests the possibility that the majority of the females in a brood die (or at least stop biting) before attaining the age of three weeks; yet some individuals may be able to survive much longer. In April, there were still old mosquitoes living and biting which probably were of the first brood which emerged during the last week of February. They seemed, however, not to have been able to lay eggs: the rain of April 6–8 hatched Brood II, but the next rain, on April 18–19, did not produce any larvae, so that the old mosquitoes had, therefore, not laid any eggs between these dates. This observation seems to indicate that all the eggs are hatched at once when inundated—which is contrary to the findings of Smith and Viereck (Headlee 1945, p. 49) for *Aedes sollicitans,* the eggs of which were only partly hatched during each inundation.

Periods in the adult life of the female. The observations given above are far from giving more than fractions of the life history of the adult female *Aedes taeniorhynchus,* but they seem to suggest the vague outline of a number of periods:

1. The emerging and the resting period (½ to 1 day).
2. The first disappearance which probably is the period of dispersal, and possibly the period of copulation (3 days).
3. The first biting period (1 day).
4. The second disappearance which is probably the time necessary for the maturing of the eggs.

5. The egg-laying.

The last three periods are then repeated a number of times. The duration of the periods refers to Brood III; it will be remembered that the days for biting were separated by 5-day intervals (June 7–8, June 12, June 17–18), and so were the days on which egg-filled females were seen: June 10–11, June 15–16, and June 21–22.

Habits of the Males

It has been mentioned that the females spent considerable time in resting places as yet unknown to us. The males are still more inconspicuous. A few hours after emerging, they leave the vicinity of the breeding waters and disappear completely except for the few minutes, morning and evening, when they swarm.

We made some efforts to find them, especially on the Meadow where the vegetation is not particularly dense and where we knew from the swarms that they were present in considerable numbers. We never succeeded in seeing any. By thorough sweeping of the grass, three or four males were found among hundreds of females of which probably the great majority had risen from their resting places to get a blood meal. The only habit of the male upon which we can report is the swarming.

Swarming. Of the different types of male swarms previously described as typical for gnats observed in Denmark (Nielsen and Greve 1950), only one was found to be performed by *Aedes taeniorhynchus, viz.,* the top-swarm. These swarms are formed close to the top of some prominent feature in the landscape, usually a bush or a tree. Most of our observations were made on the Meadow where several swarms were observed over small (2–3 m. high) *Baccharis* and mangrove bushes. In unusually calm weather, swarms may have formed over higher trees, but they were very difficult to see. If there was any wind at all, the swarms formed only over lower bushes; and with wind velocities exceeding 1 m./sec. (2 mi./hr.), the mosquitoes did not swarm above the bushes but behind them, sheltered from the wind. This is very different from the species observed in Denmark which always swarm at the highest tree tops and stay above them at wind speeds up to 8 m./sec. (18 mi./hr.) and only at higher wind speeds seek shelter behind the top.

The swarms are very sensitive to light. A beam from a flashlight will at once disperse the swarm. By moving the beam in a fast and sweeping manner, it is possible, however, to get a glimpse of a swarm before it disperses. Swarming males are also very sensitive to sound; ordinary human speech makes observation of the swarms impossible. The humming from a male *taeniorhynchus* is rather weak. Even at a short distance, it is impossible to hear the humming from small swarms except in calm weather.

The males start swarming four days after emergence, at the same age as females start biting. They then swarm, morning and evening, for a period which in Brood II was found to be 12 days, in Brood III 11 days, while for Brood IV there is evidence of two males swarming at least 14 and probably 18 days. The longevity of the males is, therefore, two to three weeks.

For all the mosquito species examined by Nielsen and Greve (1950), including *Aedes cantans, A. communis, Culex pipiens* Linnaeus, *Chaeoborus crystallinus* (De Geer), and for some chironomids, it was found that the male swarming had no direct relationship to mating, and this was found also to be the case with *Aedes taeniorhynchus.* We never saw, in the swarm, any copulation or any behavior suggesting readiness for sexual activity. It is most likely that the females had mated before they started biting, and therefore, also before the males started swarming. It might, in this connection, be worth mentioning that Brood V hatched on June 16 while its fathers (from Brood III) still swarmed and continued swarming until June 19.

The top-swarms of the above-mentioned

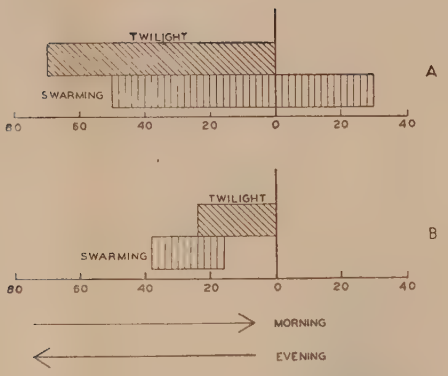

FIG. 3. Swarming of *A. cantans* in Denmark (A), and *A. taeniorhynchus* in Florida (B), in relation to sunset or sunrise, and twilight. Horizontal axis indicates the deviation in minutes from the moment (indicated by the vertical line) when the sun is at the horizon.

mosquitoes last on the average 80 minutes, from 30 minutes before sunset to 50 minutes after; in the morning, from 50 minutes before sunrise to 30 minutes after. This was observed in Denmark (56° N. lat.) where the twilight, during the swarming season for the mosquitoes, lasts 70 minutes. By twilight, we mean here, as everywhere in this paper, the civil twilight: the time when the sun is less than 6° below the horizon. At Fort Pierce (26° N. lat.), the civil twilight lasts 23–26 minutes, and we found a swarming period of about 20 minutes in the evening starting some time after sunset and in the morning ending the same time before sunrise. The morning swarms were generally somewhat weaker than in the evening, but they were symmetrical with the evening swarms in relation to the twilight. In the following we shall consider evening conditions only, but the morning observations are included, with reversed sign, in Figures 3 and 4.

For each brood the hour of swarming was fairly constant; but for broods in different seasons, there were some differences. The first swarms observed were the very large ones on Sanibel Island (off SW coast of Florida), September 9–12, 1950; these had the midpoint of the swarming time at 1917. In the last weeks of April, 1951, at Fort Pierce, we found the midpoint to be 1920, and in June it was 1943. The midpoints were 27, 28, and 30 minutes, respectively, after sunset. A still better agreement obtained with the end of the twilight, which preceded the midpoint by 4.1, 4.3, and 4.2 minutes, respectively.

This demonstrates the rigidity of the relationship existing between swarming and twilight. There was, however, a difference between the three broods in the duration of the swarms which must be explained otherwise. The swarms on Sanibel Island lasted 27 minutes; at Fort Pierce the swarms of Broods II and III lasted 23 minutes and 12 minutes respectively.

These differences in duration are easily explainable by understanding that the top-swarms are intermediate passage swarms in which new individuals are all the time replacing others leaving the swarms. Each individual stays in the swarm only a fraction of the total swarm duration. At present we have no knowledge of the factor initiating swarming, even if it is likely to be a certain rate of change in light intensity. But whatever

FIG. 4. Duration of the swarms on Sanibel Island, September, 1950 (A), Fort Pierce in April, 1951 (B), and in June, 1951 (C). The single-hatched areas are the observations of the beginning of the swarms, the double-hatched squares those of the finish. Zero on the abscissa is four minutes after the end of twilight.

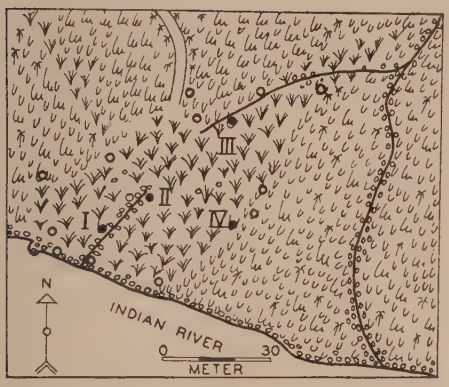

FIG. 5. Sketch map of the Meadow. Open dots are sites of swarms; black dots are swarms used in the marking experiment (see text). Other symbols as in Figure 1.

it might be, it is obvious that the duration of the swarm will express the maximum dispersion of individual variations in sensitivity to this factor. Such ranges usually have a normal frequency distribution of the sensitivities or of their logarithms. In other words: the majority of the individuals will react (start swarming) on a mean value of the stimulus, while a gradually decreasing number of individuals will react on values of the stimulus differing more and more from the mean. The greater the number of individuals exposed to the stimulus, the greater will be the range of variations expected and the greater, consequently, will be the chances of encountering extraordinarily high or low sensitivities. In the present instance, this means the larger the swarm, the longer its duration. This is exactly what was found: Brood III with only 12 minutes swarming time was a very small brood, mostly with 2 or 3 males present at a time in the swarms; Brood II had swarms with 10–15 males at a time, and the swarms on Sanibel Island were still much larger, probably with hundreds of individuals.

Marking experiment. That top-swarms actually are intermediate passage swarms has been shown for *Aedes cantans* by direct observation (Nielsen and Greve 1950). We tried to demonstrate it for *A. taeniorhynchus* by a marking experiment. Since such an experiment was likely to destroy the swarms, we did not attempt it on the first broods (II and III) for which we wanted undisturbed observations of the normal course of the swarming. In the latter part of June, swarms of Brood IV were marked with dyes, then in July an effort was made to repeat the experiment with Brood VII, using bronze powder. In the latter case, the metal powder seemed to affect the animals, and the swarms disappeared after the marking. We have thus only one experiment to report, the results of which, however, are very clear.

On the map (Fig. 5), the four most important swarm sites in the western part of the Meadow are indicated by I–IV. On June 25, the swarming males at the low mangroves (Swarms I and II) were dusted with eosin mixed with wheat flour. The swarms lasted from 1937 to 1957. The next evening all swarming males were caught; they lasted that evening from 1939 to 1957. In order to compare dusting times and subsequent catching times, the dusting times in the following discussion have been corrected by adding two minutes to the first third of the interval and one minute to the middle period while leaving the last third of the interval without correction.

The overall result was that of the 101 males caught the second evening at I and II, 82 were marked. From III, where no dusting was done the preceding day, one out of 26 males was colored. The catching was very complete as the following evening only one male was found at II (it was marked), and none were found at I and III. Swarm IV was also collected that evening, and all 17 males caught were unmarked. In the following evenings, no regular swarms were seen at these places through July 7. No observations were made on July 8, but on July 9, the swarms of Brood VI started. A sample of 17 males was caught at site I, and two of them appeared to be marked. They had thus remained at this place 14

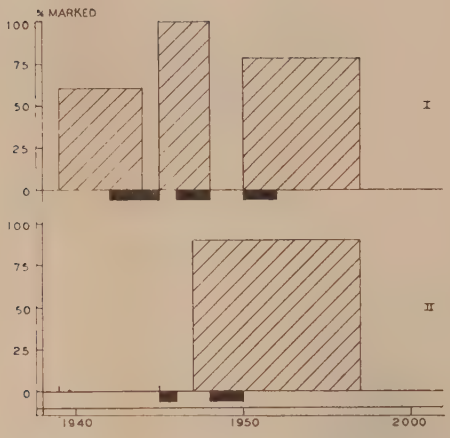

FIG. 6. Marking times (black areas) and catching times (hatched areas) in the experiment (see text).

days at least, for Brood IV marked on June 25 had started to swarm on June 21 and had probably emerged on June 17.

These observations (Fig. 6) show clearly that the same male swarms at the same place each evening and that there is hardly any exchange of individuals between swarms at a distance of about 30 m. (100 ft.). As will be seen by the following closer analysis of the data, there seems not even to have been any exchange between Swarms I and II, although they were separated by only a couple of meters.

In Swarm I, the dusting took place at 1942–1945, 1946–1948, and 1950–1952. The following evening the collections were as follows: 1939–1944 (7 marked out of 11 caught), 1945–1948 (28 caught, all marked), and 1950–1957 (27 marked out of 31 caught). Swarm II was dusted at 1945–1946 and 1948–1950; the following evening collections were at 1939–1945 (10 caught, none colored), and at 1945–1957 (19 marked out of 21 caught).

Two points are especially interesting in these results. The only case of catching 100% marked individuals (middle period, Swarm I) is from the only period which corresponds to a dusting period the night before; and the only period in which none of the mosquitoes were marked (first period, Swarm II) corresponds to a period when no dusting took place. In spite of the small numbers of individuals involved, there can hardly be any interpretation but the following: a male will not only swarm every evening at the same place, but within the duration of the swarm, it will make its flight in the same period according to its individual sensitivity to the acting stimulus.

In the middle period of catching in Swarm I, 1945–1948, all the individuals were marked, but no dusting took place 1945–1946 the night before; this could indicate that no individual had arrived, swarmed, and again left the swarm during this minute. In other words, each mosquito must stay in the swarm for more than one minute. The swarm had lasted for three minutes before the dusting was started, but in the corresponding period the next day, only 7 of 11 mosquitoes were marked, which might indicate that some had left the swarm before the dusting started. This could be interpreted as indicating a stay in the swarm of less than 3 minutes, and probably considerably less because as many as four out of 11 were unmarked. The individual male's stay in the swarm can then be estimated at 1½ minutes. It corresponds for the fully developed swarms from Sanibel Island to 5.6% of the total duration of the swarm (27 minutes). In Denmark, *Aedes cantans* individuals stayed in the swarm about five minutes of the 80 minutes total duration or very nearly the same proportion: 6.25%.

If the duration of the swarm is an expression of individual ranges of sensitivity to the acting stimulus, one should expect that there would be more individuals in the middle part of the swarming time than at the beginning and finish. Direct observation showed a definite increase in the number of mosquitoes during the first minutes of swarming, but, unfortunately, it soon became too dark to make reliable counts. Assuming that each male stayed 1½ minutes in the swarm, calculations based on catchings at

various portions of the swarming time indicate that the number of mosquitoes joining the swarm each minute increased from one or two to ten and then decreased again.

Acknowledgments

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We wish gratefully to acknowledge the permission given by P. McConville to use his property on Fort Pierce North Beach as a study area. Last, but not least, we wish to thank W. V. King, U. S. Bureau of Entomology and Plant Quarantine, Orlando, for stimulating discussions.

Summary

The observations of *Aedes taeniorhynchus* in Florida above described suggest the following conclusions with reference to the life history and behavior of this mosquito:

1. The newly-emerged mosquitoes remain for 12–24 hours in the vicinity of the pool from which they emerged; we did not find any difference in the time of emergence between males and females.

2. During the following three days, they disperse over a considerable area.

3. The adults spend most of their life at resting places as yet unknown to us.

4. The biting shows a 5-day cycle, being most intensive when the females are about 4, 9, and 14 days old.

5. Females ready to lay eggs perform a special flight. Such flights occur when the females are about 7, 12, and 17 days old as a 5-day cycle.

6. Most of the females seemed to live 3–4 weeks and some much longer; old females may bite but do not lay eggs.

7. All eggs present in an area seem to hatch at the first inundation.

8. Females ready to lay eggs are the only adults found not to be repelled by light. The occurrence of males in light traps is not yet understood.

9. Matings were not observed in the swarms and probably took place during the first days of adult life, previous to the swarming period.

10. Males form top-swarms evening and morning, from the age of 4 days until they are 2–3 weeks old.

11. The top-swarms are transient passage swarms in which each single individual participates only a fraction of the total duration of the swarm, probably 1½ minutes.

12. The duration of the top-swarms depends on the range of variation in individual sensitivities to the (unknown) acting stimulus, and may vary from 12 minutes for a small swarm to 27 minutes for a large one.

13. The midpoint of the swarming time is on an average 4 minutes after the end of civil twilight in the evening and 4 minutes before the beginning of the twilight in the morning.

14. Each male swarms each evening and morning at the same place and at the same time in relation to twilight.

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FACTORS IN CYPRESS DOME DEVELOPMENT [1]

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INTRODUCTION

The dome-like cypress groves common in the flatwoods and savannas of peninsular Florida arouse interest in the lay traveller and the scientist alike. The observer soon notes that the domes are formed by the confluent tops of crowded trees which, beginning with the short ones at the outer edge, stand progressively taller toward the center of the swamp. See Figure 1.

Several writers have published their interpretations of the nature of these domes. Harper (1927:117) makes the following statement: "Anyone seeing such a pond for the first time might imagine that the small trees at the edges were young ones and that the cypress growth was spreading. But the cypress never voluntarily invades dry land, and there is no reason to suppose that the climate is becoming wetter or the water deeper. The little trees at the edges have probably had just as much time to grow as the large ones in the middle, but they must be dwarfed by some unfavorable soil condition. The reason for all this, however, is not known."

Contrarily, Kurz (1933:56) concludes, on the basis of growth ring studies, that the outer smaller trees are actually younger than the inner ones. He explains the dome-shaped profile as follows: "Close observation brings out the fact that there is a high rate of premature mortality in the trees near the edge. The nearer one approaches the edge the higher is the mortality.

"New shoots or seedlings replace the dead ones and they themselves in turn meet death. Toward the deeper water, the number of fatalities and replacements diminish so that nearer the middle the individual trees are progressively older and larger. This decrease in fatalities and consequent increase in size is so proportionate to the center that whole groves, sometimes a quarter of a mile or more across, loom like huge, symmetrical domes or distant mounds on the horizon."

Vernon (1947) contends that cypress domes in the peninsula of Florida are really the result of young trees spreading into the peripheral area of a growing pond. He postulates a successful invasion of the surrounding site as it becomes favorable for cypress germination and survival. The expansion or enlargement of the site suitable for cypress he attributes to a gradual deepening of the water in the basins. In his explanation (p. 99) of a gradual deepening of water, he concludes: ". . . the gradual rise of water level and regional deepening of these ponds and subsequent development of cypress domes . . . is indicative of a steady rise in sea level throughout the Recent." This conclusion that cypress domes are related to a rising sea level and that therefore these domes may be cited as additional proof of a rising sea has led the writers to re-examine cypress domes.

The writers investigated domes of bald cypress (*Taxodium distichum* (L.) Richards) and pond cypress (*Taxodium ascendens* Brongn.) in localities ranging from the Everglades, the St. Johns River savanna, and the flatwoods of peninsular Florida to the flatwoods or higher terrain of the northwestern section of the state.

BALD CYPRESS DOMES

In the St. Johns River savanna, within a distance of 4 miles east of Deer Park, the writers explored 3 bald cypress domes on the Julee Rauleson ranch which is north of U. S. Highway 192 and on the Brevard-Osceola county line. In the same locality, 13 more bald cypress domes were investigated on the George Kempfer ranch which

[1] Contribution No. 45. Department of Botany, Florida State University.

FIG. 1. Bald cypress dome in St. Johns River savanna on Rauleson Ranch east of Deer Park, Florida, U. S. Highway 192.

is to the south of U. S. Highway 192 and stretches across two counties—Osceola and Brevard. According to Gunter (1948) an elevation marker in this immediate vicinity is only 28.17 feet above sea level. A system of canals and ditches leading into, or away from cypress swamps, or connecting one swamp with another, has resulted in an average lower water table of this low flat land. After heavy rains, the water may actually reach higher levels than prior to the artificial drainage. However the writers did not see much evidence to indicate that domes are expanding in response to temporary higher water increasing the pond area. But granted that there is some tendency toward expansion due to the temporary rise in water level, it obviously is not attributable to a rising sea level but rather to local drainage modifications. Whatever the influence of local drainage modifications, it is a factor apart as far as doming influence is concerned. In all the domes examined, the authors found either old or new signs of injury and sprouting of cypress trees. The nearer the edge of the pond they stood, the more frequent and severe was the injury. These injuries were caused by two agents, namely, fire and animals. Of these two, the former seems the more common.

The fire injuries are of two types: ground fires which damage the tree low and often cut the tree back to the ground, so to speak, and result in charred and more

or less chunky stumps. Regeneration will produce from one to twenty-five or thirty sprouts from a single base (Fig. 2). According to frequency of burning, these shoots will in turn be killed back and new ones replace them. The second type of injury by fire as revealed by more or less blackened tips of saplings or sprouts is caused by crown burning. Usually shoots killed in this manner are replaced by a lateral branch which takes over as the dominant. It follows that the trees nearest the edge of the dome, where ground and grass are the driest, are in the greatest danger of fire. On the contrary, the trees nearest the center, standing in water or damp substratum, are not injured by fire as often or as severely. Consequently, they develop into larger trees more rapidly than the outer ones. Moreover, their thicker bark will tend to protect them. In short, from the edge toward the center the fire is less and less effective in keeping down the height of trees. In the Deer Park vicinity, there has been some effort to control burning or to eliminate fire entirely. However, the practice is not uniform among the cattlemen. In any event, the domes are clearly the result of old or recent fires.

Fig. 2. Fire damage and sprouting from fire injured stumps of pond cypress near Loyce, Pasco County, Florida.

FIG. 3. Bald cypress with terrace in foreground formed by uniform growth of the saplings as a result of local draining and reduction of fire. Rauleson Ranch, east of Deer Park, U. S. Highway 192.

The second type of injury was due to cattle or deer rubbing against the saplings with the result of breaking off or severely bruising the leading shoots and branches. Local cattlemen attribute this type of injury to the attempts of the cattle to brush off flies, or to buck deer's efforts to rub their horns. Just how important this mutilation by animals is in producing the symmetry of a dome, the writers do not know. Whatever the importance, it is confined mostly to the peripheral zones.

In one instance, the writers found what appeared to be a definite case of cypress expansion due to a rising water level. This was a cypress pond whose natural drainage was blocked by the highway grade and a sluggish plant-clogged road canal. Here young cypress were obviously invading the adjacent area. But curiously enough their uniform height presented a canopy which abutted against the older trees like a terrace—not a slanting dome. See Figure 3. Damming some years ago and freedom from fire since seem to be the explanation. One other dome on the Julee Rauleson property showed signs of expansion. Smaller trees were establishing themselves on the outer fringe, so that this dome is taking on a very gradual sloping profile toward the edge. Young saplings scarcely checked by fire are actually invading surrounding land. Freedom from fire and local drainage modification seem to be the answer here; or one of these causes alone could be responsible.

All of the other domes that the writers investigated in the St. Johns River savanna and in the slightly higher flatwoods of Deer Park and immediately westward were clearly the product of fire. It is difficult to see how there could be a general and

permanent rise of water table due to rising sea level where artificial drainage is effectively helping sluggish natural drainage to lead away ground and surface water.

Pond Cypress Domes

Pond cypress (*Taxodium ascendens* Brongn.) is the usual species encountered in depressions or sluggish creeks of flatwoods, or in ponds of sandhill topography. The writers examined a number of these in various localities from the middle peninsula to the northwestern section of the state. As a matter of fact, several pond cypress domes were examined in slightly higher sandy terrain south of Deer Park (Kempfer Ranch) which adjoins the St. Johns River savanna immediately to the west. The nearest comparable elevation given by Gunter (1948) for this higher flatwoods or low scrub is 41.9 feet on U. S. Highway 192, 9 miles east of Holopaw, Osceola County. The influence of injury by fire and mutilation by animals was obvious.

About 100 miles westward from Deer Park and across the peninsula in the vicinity of Loyce, Pasco County, pond cypress domes are common in the flatwoods. Elevations of this vicinity run 63.5 feet near Loyce, situated approximately 6 miles north of the dome; 73.50 feet at Denham, 10 miles south of the dome; and 75.5 feet at Fivay, 5 miles west of the dome. It will be noted that this area in general is well above sea level. Charred stumps and trunks everywhere indicated plainly the importance of fire as a dome former.

Still other pond cypress domes were studied in localities extending from the vicinity of Naples in southern Florida to west of Ft. Walton in the northwestern part of the state.

The following table includes the dome sites of the present paper and the nearest comparable elevation records taken from Gunter (1948).

Table I. *Areas studied and approximate elevations*

County	Dome locality	Nearest comparable elevation	Location of bench marks
Brevard and Osceola	Bald cypress, 1½ to 3 mi. e. of Deer Park. Both sides of U.S. Highway 192.	28.17 ft.	2 mi. e. Deer Park on U.S. Highway 192.
Brevard and Osceola	Pond cypress, on Kempfer Ranch 2–3 mi. s. Kempfer residence at Deer Park.	41.9 ft.	9 mi. e. Holopaw on U.S. Highway 192, 2 mi. n. of Deer Park.
Collier	Pond cypress, 7–8 mi. n. Naples on e. side U.S. Highway 41.	10.7 ft.	6.7 mi. n. Naples, over one mi. from dome.
Levy	Pond cypress, 3 mi. nw. Levy-Marion County line on Fla. Highway 336 Both sides of the road.	61.95 ft.	Junction of Fla. Highways 336 and 40 (4 mi. se. of dome).
Orange	Pond cypress, n. of Fla. Highway 50 near W. Orlando city limits. An unsymmetrical dome.	100.7 ft.	3.9 mi. w. Orlando Coastline RR Station
Pasco	Vicinity of Loyce, just east of Gowers Corner.	75.5 ft. 63.5 ft. 73.5 ft.	Fivay (15 mi. w. of dome) 2½ mi. n. Loyce (6 mi. n.) Denham (10 mi. s. of dome)
Santa Rosa	Pond Cypress, 7. mi. w. Navarre south side U.S. Highway 98.	34.7 ft.	3.8 mi. w. Navarre, approx. 3 mi. s. of dome.
Washington	Pond cypress, 3.7 mi. e. of Caryville, n. of U.S. Highway 90 and at Washington-Holmes County line.	103.6 ft.	3 mi. e. Caryville on L. & N. Railroad.

Discussion

All well-defined domes, whether in very low or relatively high elevations, in southern, middle, or northwestern Florida, follow a strikingly similar pattern: in each the peripheral trees were the product of regenerative shoots. These shoots, sometimes as many as 25 or 30 from a common base, do not represent single-stemmed uninjured saplings successfully invading adjacent areas. Only here and there does one see small saplings comparable in size which so far have fortuitously escaped injury by fire. Invasion on the part of these periodically burned peripheral trees is greatly retarded if not entirely stalemated.

Vernon (1947) points out that Kurz (1933) was unable to explain the dying back of trees in the peripheral shallow water. In the present work the writers have found that fire is the agent of destruction and retardation. Basins and depressions of Florida which support cypress domes undergo a considerable range in water level fluctuation. At times there may be prolonged standing water; at other times the more shallow depressions may be dry to the interior. This periodic rising and falling of the water has a definite effect on the germination of cypress seeds and on the survival of the seedlings. Gradual recession of the water makes possible the germination of cypress seeds over a large part of the basin. Factors in the germination of cypress seeds have been discussed by Demaree (1932) who shows that they will not germinate under water. Ideal conditions for germination occur just at the water's edge. On the other hand, rising water may cover the young seedlings long enough to kill them.

Water levels influence the intensity of fire within the dome and thus the survival of the cypress trees. The drier the basin becomes, the hotter the fire will be and the nearer to the center of the dome it will penetrate. The replacement of lumbered trees within the dome and the invasion of the surrounding site are met, therefore, by a double hazard: drowning and burning. A low water level favors seed germination and growth but at the same time increases the fire hazard. A high water level reduces the influence of fire but, if prolonged, results in the drowning of the

Fig. 4. Interior of second growth bald cypress dome with a few scattered larger and older trees which escaped cutting.

seedlings which are covered. From this it follows that the establishment of the seedlings and their survival during the first few years is governed primarily by water levels, but the dome shape of the canopy is fashioned by fire which exerts less influence progressively from the edge of the swamp to the center.

Vernon (1947) also argues that, ". . . a high mortality rate progressively nearer the periphery does not explain why older trees are not scattered throughout the dome, as would be expected." The authors meet this objection by pointing out that trees 24 to 36 inches in diameter above the buttress are common in these domes (Fig. 4). A spot check of 12 domes showed that the average number of such trees per dome was 9. Even more impressive are the large stumps which occur from the center to the edge of many of the ponds. Stumps up to 6 feet in diameter were found in the bald cypress domes at Deer Park. The larger the stumps, the more nearly were they completely decayed.

Heights and diameters of the trees currently constituting the domes indicate that the majority are less than 100 years old. Except for those mentioned in the paragraph above, they are seldom more than 12 to 15 inches in diameter at breast height. Those which are larger are usually pecky or hollow and beset with many short, low, dead branches. Unsuitable for lumber, these remnants stand in sharp contrast with the surrounding slender, unbranched poles. This lower branching may have been induced or maintained by the better light conditions following the removal of neighboring trees for lumber.

We may take the evidence presented in the preceding two paragraphs as proof that in former times, before lumbering, the dome sites were occupied by larger and older trees and that the present day cypress domes consist of second growth. The presence of large stumps in the outer zones of the basins indicate that water has filled these ponds to the present boundary from time to time long before the beginning of the present secondary growth domes. It is not likely that the general rise of water level, due to an encroaching sea, was initiated with and paralleled the repopulation on the part of cypress or that this gradual filling process was a repetition coincidental with secondary invasion of cypress in recent times. Furthermore, some of the cypress basins are up to 25 miles removed from the sea-coasts. Their elevation ranges from 11 to 103 feet and the geological structure underlying them varies greatly according to locality. Therefore, it does not seem acceptable that such diversities in distance, elevations, and geological structure could bring about a uniform deepening in water basins. Yet that is what we would have to accept if we were to account for the cypress domes situated throughout the state on the basis of a rising sea level.

Summary

1. Cypress domes are formed by the confluent tops of crowded trees which, beginning with the short ones at the outer edge, stand progressively taller toward the center of the swamp.

2. Cypress domes, except in special cases, are not expanding cypress swamps; successful invasion of the peripheral treeless areas by cypress is a rare occurrence. The dome profile gives the false impression of centrifugal invasion of the higher ground by young seedlings. These small trees are the results of stunted growth or repeated sprouting due to periodic burning. The closer they are to the edge, the more severe the fire and the shorter are the trees or sprouts.

3. Fire, more or less counteracted by water level fluctuation in the basins, controls the shape of the domes. During periods of low rainfall, the periphery of the swamp is the first part to become dry and it experiences longer and more severe effects of the drought than does the interior. From the edge toward the center, the surface water is progressively deeper and more nearly permanent. Injury by

fire is more frequent and more severe in the outer portions of the dome where the trees and regenerating sprouts have the lowest stature. Toward the center, with the reduced fire hazard, the trees are progressively taller, thus forming a dome.

4. Cypress domes are found as far as 25 miles inland and at elevations of up to 100 feet. They are underlain by thick and diverse geological formations. These cypress swamps are not expanding in area.

5. Cypress dome swamps reveal nothing to indicate a general rise in water level. As far as cypress dome development is concerned, the influence of a rising sea level may be dismissed.

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TERRITORIALITY IN THE GREEN FROG, *RANA CLAMITANS*[1]

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INTRODUCTION

The concept of territoriality was developed only recently. As early as the eighteenth century, workers observed the defense of restricted areas by birds but it remained for Howard (1920) to propose a theory of territoriality which gained wide recognition. Since, territoriality has been studied in great detail and it has been found that several kinds of animals, for example, many mammals (Carpenter 1934; Burt 1940), birds (Nice 1941; Lack 1939), lizards (Evans 1936), fishes (Noble and Curtis 1939), and some invertebrates (Crane 1941), restrict their reproductive activities to areas defended against intruders. It is generally agreed that territoriality is the active defense of an area which is used in some phase of the breeding cycle.

Even though several species of amphibians restrict their activities to definite home ranges (McAtee 1921; Breder *et al.* 1927), there are many reports in the literature which state that territoriality is absent among them (*e.g.*, Collias 1944; Davis 1949). However, I am unable to find record of actual attempts to learn whether this phenomenon really does occur among amphibians. This report is offered to fill partially this gap in our knowledge. It is one aspect of an ecological study of the green frog (*Rana clamitans*) made in 1948 and 1949.

It is a pleasure to acknowledge my indebtedness to Frederick H. Test, who has directed this investigation. I am also grateful to the members of the Statistical Research Laboratory at the University of Michigan, Cecil C. Craig and Paul S. Dwyer, for their valuable suggestions concerning the statistical treatment of data; and to Eugene P. Odum for his critical reading of the manuscript.

[1] This paper is extracted from a dissertation submitted at the University of Michigan. It was expanded and prepared for publication while the author was on the staff of the University of Georgia.

STUDY AREA AND PROCEDURE

In making this study of spatial relationships of the green frog a site located about two and a half miles east of Ann Arbor, Michigan, and about a quarter of a mile south of the Huron River provided most of the data. The area studied was approximately 60,000 square meters and consisted of a pastured field with three small ponds (Fig. 1). These ponds were solely dependent upon rain as their source of water and since they had gently sloping banks, their areas directly reflected the rainfall. The western pond was about 2,400 square meters in size and through the year had an average greatest depth of 30 cm. When deeper than 33 cm. it overflowed into the middle one which was about 6,500 square meters in surface area and 53 cm. deep. When the water in this pond was above 61 cm. it drained into the east one, which had an area of about 2,000 square meters and contained water only in the spring and after heavy rains. At these times its greatest depth averaged about 20 cm. Any increase in depth caused it to drain into a small stream which meandered through the eastern part of the area and entered the adjacent woods. This stream was mostly about a meter wide and 7.5 cm. deep, with some deeper pools averaging 30 cm. Its banks were about a half meter high. These ponds and the stream provided excellent habitat for green frogs.

The rich black soil in the vicinity of the ponds and stream supported a dense belt of *Carex* which completely surrounded the ponds and stream. These sedges attained an average height of 60–75 cm.,

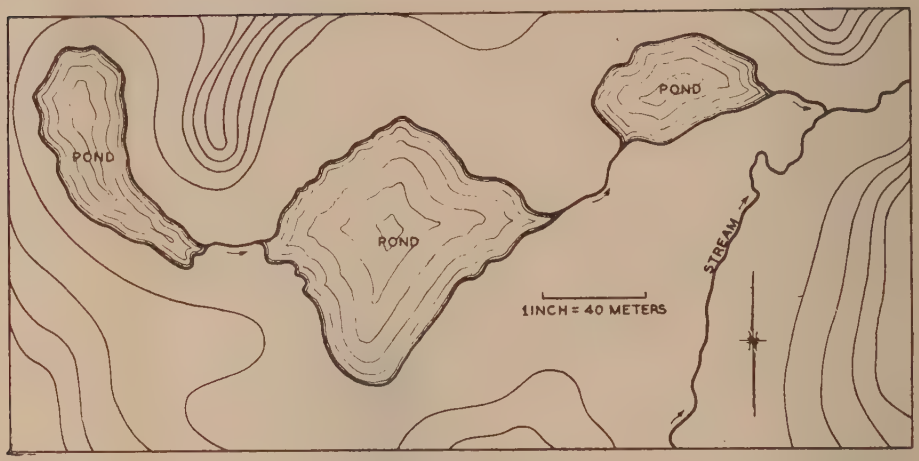

FIG. 1. Map of the Hogback study area. The land contour lines are for a five-foot interval. Direction of water flow is indicated by arrows.

forming a dense ground cover because of their rank growth and the accumulation of dead stems beneath the growing plants. Patches of *Scirpus cyperinus, Iris versicolor, Typha latifolia,* and *Phragmites communis* were scattered throughout the belt of *Carex*. Toward the center of the ponds the sedges were gradually replaced by *Acorus Calamus, Sagittaria latifolia, Sparganium chlorocarpum,* and *Eleocharis*. During the spring the surface of the ponds and stream was covered by *Lemna*. By early summer the *Lemna* disappeared, and emergent vegetation increased until by late summer dense cover for frogs was provided in the ponds by *Polygonum natans* and *Sagittaria latifolia* and in the remainder of the *Carex* zone by *Polygonum* and *Bidens*. After the disappearance of the *Lemna,* the stream was relatively free of vegetation.

Except for the moderately dense stand of *Quercus alba, Q. velutina* and *Carya ovata* along the western border of the area, scattered *Crataegus* were the most prominent plants beyond the *Carex* zone. To the north and south the study site was continuous with open pastures spotted with *Crataegus*. A dense stand of planted *Pinus Strobus* covered about 40,000 square meters along the eastern side of the area. Along the western part of the study area the *Quercus-Carya* woods extended northward and nearer the river was replaced by *Ulmus fulva* and *Acer Negundo*.

In addition to *Rana clamitans,* the following amphibians bred in the quiet waters of the ponds: *R. pipiens, R. sylvatica, R. palustris, Acris gryllus, Hyla crucifer,* and *H. versicolor*. Many immature *R. catesbeiana* were captured in the ponds but no breeding activity was noticed.

Grazing by cattle occurred on the study area; however, this was not a major disturbance to the frogs.

GENERAL METHODS

In searching for frogs the usual procedure was to walk more or less systematically over the entire study site each week. When a frog was seen it was cautiously approached and generally captured by a quick thrust of the hand. A net was used to make captures during the early part of the study but was abandoned when its use resulted in injury to a frog.

Nocturnal capture of frogs was remarkably easy since they made no attempt to avoid an approaching light. A headlight, operated by four flashlight batteries, proved to be satisfactory illumination for

measuring specimens and writing data, but was inconvenient for locating frogs because much turning of the head was required. For searching, a hand lantern, operated by a six-volt battery, provided sufficient light to see frogs easily.

Each frog was marked for future recognition by cutting its toes with scissors, care being exercised that the web between them was not seriously injured. As a result, no significant loss of blood occurred and the swimming power of a marked frog was not noticeably impaired. A standard type of marking was used in which the distal phalanx and about one half of the next were removed. The cutting of a phalanx was chosen because most natural losses occurred at joints. On no occasion was regeneration of excised digits observed.

The following method was used in marking toes. Units were indicated on the left hind foot, where a marked first digit stood for number one, a marked second digit for number two, etc. For units larger than five, combinations of two toes, the fifth and another were used; *e.g.,* the fifth and first toes were excised to denote number six, the fifth and second for number seven, etc. Similarly tens were indicated on the right hind foot and hundreds on the front feet (Fig. 2). This plan permits a series of 6399 individuals to be marked.

Raney's criticism (1940) of the toe clipping method, that difficult bookkeeping results when more than a few dozen specimens are marked, did not appear to be valid. George (1940) successfully used the toe cutting method in a study of Louisiana bullfrogs, though his numbering scheme was different. The one used in this study is a modification of that employed at the Institute of Human Biology, University of Michigan, to mark mice.

The above described plan was very satisfactory with but few exceptions which involved the marking of a single hind foot, especially when but a single toe was excised. For these occasions it is recommended that a special designation, such as excision of the second and fourth digits, be used as a zero marking on the other hind foot. Thus confusion arising from capture of a frog with an injured foot would be greatly eliminated.

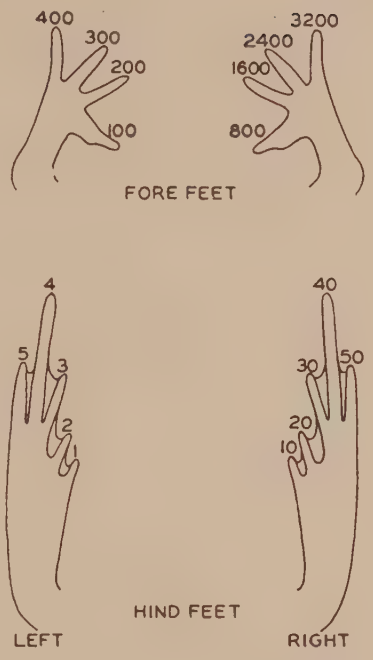

FIG. 2. Schematic drawing of feet to show system of assigning serial numbers.

As an aid in studying the movements of frogs the study area was surveyed by compass, and markers were placed at ten-meter intervals forming a grid, with numbers assigned to one ordinate and letters to the other. Originally the markers were pieces of 16-gauge iron wire, 60 cm. in length (or longer when required by deep water), and looped at one end where water-proof tags were attached. On each tag were a letter and a number identifying the location of the marker. Because cattle tended to chew the paper tags and to trample the wires, wooden stakes (2.5 cm. × 2.5 cm.) were gradually substituted and locations were written on them with a black china-marking pencil. This extensive system of markers permitted

the location of each frog to be accurately obtained by observing its distance north or south and east or west from the nearest marker. In addition to the above-mentioned data, measurements were taken from snout to vent and of the tympanum diameter of each captured frog. Also the sex of each adult specimen was noted at the time of capture, the tympanum measurement proving useful for dubious cases, particularly for recently matured frogs. Because the nature and intensity of ventral markings and dorsal coloration varied considerably among individuals, general color patterns and markings were noted. All these characteristics provided a check on the identity of recaptured specimens.

Each frog was released at the place of capture, and information pertaining to the nature of the situation was recorded: kind and density of vegetation, and depth of water. General weather data such as sky condition, precipitation, wind velocity, air and water temperature were taken. In addition, date, time, behavior, and general remarks were recorded. At no time were frogs removed from the area and care was exercised continuously to preserve the naturalness of the study area.

Analysis of Data

At the onset of the breeding season, about the first week of May, there was an obvious absence of adult males from their usual places along the banks of the stream. They were then found in the ponds and lakes or else in the quiet waters of larger pools along the stream, where they spent much time calling. The partly-submerged males called most actively at night from sites near the shore or from matted vegetation farther out. Vocalization generally stopped at sunrise but sometimes it continued into the day, especially if the weather were cloudy and rain were imminent. Otherwise, only scattered calls were heard. Within the next two to four weeks most males left the temporary calling sites along the stream and formed large congresses in the more spacious ponds and lakes. Here most males stayed until about the middle of August.

Although vocalization was a typical part of breeding behavior, green frogs were heard in their habitat along streams as early as April 13 and as late as October 18. There the calls were usually infrequent, given at irregular intervals with no chorus formation and often from positions underground: in muskrat burrows, under overhanging sods, or in root entanglements of trees undercut by streams. As no additional signs of breding activity were observed in the above-mentioned situations, these times were not included as a part of the breeding season.

Females did not spend so much time at the breeding places. They stayed along the streams until they were ready to spawn, when they made their way to the ponds occupied by the males. As censuses of the area could not be complete and the periods of collection were usually a week

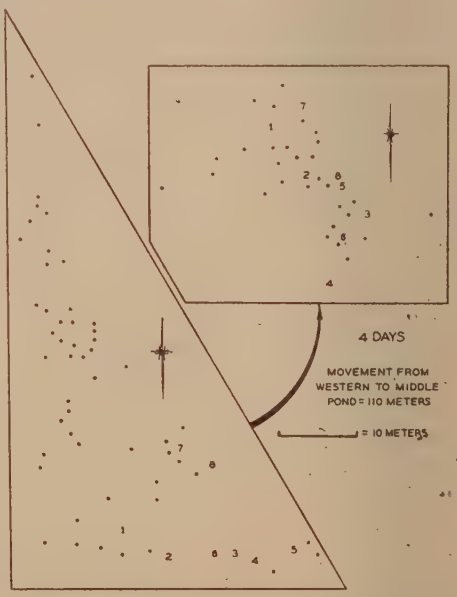

Fig. 3. The spatial relationship of adult males in the breeding ponds as shown by locations of all captures on July 8 and July 12, 1949. Individuals captured on both dates are indicated by numbers, others by dots. Boundaries are not those of ponds.

FIG. 4. The spatial relationship of adult males in the breeding ponds as shown by locations of all captures on May 30 and July 8, 1949.

apart, it was difficult to establish the length of time females were in the breeding ponds and the rate of travel of frogs going to and from the area. However, the data suggest that females were in the spawning places from a few to possibly 34 days. Judging from the smaller number of records of females taken at the breeding sites, only 13 captures of 9 females in 1949, it is doubtful if the average female spent more than a week in the breeding habitat.

In 1949 at the breeding area 148 adult males were captured 270 times. Seventy two (48 per cent) of these frogs were captured more than once while 13 (9 per cent) were captured from four to six times.

In the breeding season, males occupied most of each pond except the very deep parts, where no vegetation grew, and the very shallow zone along shore. Usually during times of active calling at night, males were readily approached and captured. My presence did not seem to be a major disturbance to them for their calling was uninterrupted. In daylight, however, frogs were approached only after exercising great caution and even then seldom captured. As soon as my approach was detected all vocal activity stopped, with the result that practically all observations of breeding males were made at night.

The calling frogs were so greatly inflated that they lay on the surface of the water, with their legs outstretched or sometimes resting upon vegetation. Occasionally one would swim about a half

meter or so, seemingly only to get on some vegetation, then resume calling. When closely grouped, the frogs were spaced at surprisingly uniform distances of about two to three meters; however, a few were captured as close as 0.3 meter.

Because of irregularity in the intervals between capture and in the number of frogs taken each week, no fixed spatial relationships among breeding males were detected at the time of collection. However, when movements of individuals were plotted, it was noted that some frogs taken on the same days made approximately the same movement and often maintained the same general position with regard to one another. Because of the frequency with which this occurred all records of individuals taken on the same days were plotted as shown in Figures 3 and 4. Their distributions suggested that two social phenomena were present: (1) a clustering effect, shown by certain frogs tending to remain together and (2) orientation, in which some individuals seemed to have the same general spatial relationship with regard to one another. In order to test these interpretations quantitatively, the following methods were used.

For convenience each frog which was captured on two different days was reassigned a low number (from one to thirteen) in addition to its regular serial number. For example, frog number one in Figure 3 is the individual with the lowest serial number and is not the same individual in Figure 4.

In order to gain some idea of the extent of the clustering effect, records of all frogs captured on the same days were examined for persistent groups, and then the probability that a particular group would be maintained on the second day was determined by the following procedure.

(1) It was assumed that an individual was as likely to be in one part of the pond occupied by frogs as in another.

(2) One frog of a persistent group was randomly selected and used as the center of a circle drawn to include the same group on the second day of capture. The area of the circle was then ascertained.

TABLE I. *Number of frogs in clusters that maintained their integrity between successive dates, and the probability that the contagious distribution is accidental*

Dates	Area occupied on second date by:		Approx. ratio of areas	Frogs in clusters	Probability of accidental clusters
	All males	Cluster			
July 8–July 12	1,360	200	1/6	5	.0008
May 30–June 6	660	110	1/6	3	.028
June 6–July 8	900	50	1/18	3	.003
May 30–July 8	900	50	1/18	4	.0002
May 30–June 6	660	100	1/6		
July 8	900	20	1/45	2	.040

(3) The total area of the pond actually occupied by males on the second day was ascertained from the locations of captures. If all the pond was not censused, its total area utilized was estimated not only from the locations of captures but also from vocalizations heard at that time.

(4) The fraction of the total area occupied by the cluster on the second day was determined; it is assumed that this fraction is the probability that two of the frogs in the group would be located in the circle. It was squared, cubed, etc., according to whether three, four, or more frogs were present in the cluster circle on the second day (Table I).

It should be noted that estimates of the areas occupied by the clusters were purposely liberal while the estimates of the total area occupied by all frogs were conservative. Other approaches could have been used, but the results obtained by this conservative method gave such highly significant probabilities that there can be no doubt about the validity of clustering behavior.

That the relative positions of certain frogs should be so consistently maintained is indeed noteworthy. It is surprising that there was not more flux in so dynamic a population for there were several factors which operated to alter the spatial relationships of frogs in the breeding ponds. A few of these will now be mentioned. (1) The breeding males did not

form a stationary population in one particular pond throughout the season. In moving from one pond into another the population had to adjust itself to the size and shape of the available breeding area in the new pond. (2) There is a relatively great turnover of frogs resulting from predation (Noble 1931; Pope 1946, 1947). (3) Simultaneous observations of the whole area could not be taken. (4) Frogs shifted in their positions as a result of my attempts to capture them. (5) Participation in amplexus may have caused males to lose their locations in the breeding populations, especially if the population were moving. In addition (6) it is estimated that about 75 to 80 per cent of the frogs present in the ponds at the time of each collection were captured, but even this shows the incomplete nature of the records.

No doubt, other factors impose changes in the spatial relationships of males as shown by records of recaptured frogs. The striking feature of these data is that they do not show a random mixing of breeding males; instead there seems to be some organization within the breeding congress. The entire breeding population did not prove to be closely integrated, but certain small groups of two to four or five frogs maintained their spatial relationships for as long as 43 days. Of the three groups of two frogs, each of which was taken on three different days, both individuals showed similar movements, thus preserving their spatial relationship to one another as indicated at the time of first capture. Some of the frogs may have been associated with more than one of the small groups and thus have accounted for the more extensive organization shown in Figure 4. In a dense population of frogs it is conceivable that the overlapping of group associations may be so extensive that the entire population would be organized for a short time (as shown in the analysis of orientation). How frogs maintain their positions during movement is a subject for conjecture; vocal and visual cues may have been responsible, the latter, especially, during overland movements. Clearly, more observations are necessary before spatial relationships of frogs can be thoroughly understood.

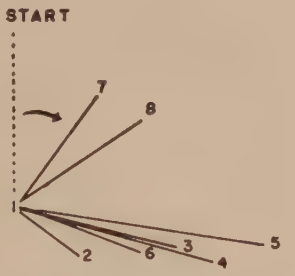

FIG. 5. Method of drawing vectors to study orientation of males in the breeding area.

In order to study the position of a frog with regard to others in a cluster (which I will refer to as "orientation"), the sequence of the numbers on the maps was ascertained by starting arbitrarily with frog number one and by noting the order in which the other numbers were crossed by vectors. As these vectors started from the twelve o'clock-position and went clockwise around frog number one (Fig. 5) others were encountered in this sequence: 7, 8, 5, 3, 4, 6, 2. The same procedure was used on the map of the second day of capture and then the sequences of vectors were compared, next the number of frogs having the same position in both sequences was noted, and finally the probability of more frogs having the same position in both sequences was determined from Feller (1950:68, Table 1). His method is an application of the classical matching problem in which we are concerned with the probability of m matchings (P_m) out of N possibilities when only chance causes are operating. This has been discussed by Feller in terms of probabilities of m correct guesses in calling a deck of N distinct cards.

Analysis of these data (Table II) suggested that orientation is of short duration; this is indicated by the significant probabilities obtained for the examples having short intervals between captures, .004

TABLE II. *Probability of the orientation of male green frogs captured on the same days in the breeding area*

Days between captures	Distance moved (meters)	Frogs captured on both dates	Frogs with equal ranking	Probability that number of matchings will equal or exceed number observed
4	110	8	5	.004
7	7	5	2½	.167
12	16	9	1	.632
32	85	3	1	.500
40	110	13	2	.264
43	110	6	1½	.452

for a period of four days and .167 for seven days. On the other hand, examples involving longer intervals did not yield any significant probabilities. Thus orientation is temporary and seems to vary inversely with the time between captures. The distance over which movement had occurred did not seem to be a contributing factor to a change in the arrangement of the individuals This is shown by the fact that when the very significant probability of .004 was obtained the frogs moved 110 meters; meanwhile, another group which moved but 16 meters showed a high (not significant) probability. It should be kept in mind that the above-mentioned lengths are average minimum distances over which the frogs moved. Accordingly the data are meaningful only in that they show orientation can be maintained even when extensive movements are made.

DISCUSSION

The evidence presented in this paper clearly indicates that a sort of social organization is present among breeding male green frogs. This organization seems to be a type of territoriality and the reason for thinking so will be explained in the discussion which follows.

According to Nice (1933), an animal has territoriality if it demonstrates advertisement, isolation, intolerance, and fixation. In view of the above mentioned criteria, the data pertaining to the green frog were evaluated. There certainly was "advertisement" for during most of the breeding season, the frogs called all night long and could be heard at a distance of more than a half mile. Each calling frog was so greatly inflated that it usually lay in open view on the surface of the water.

Actually "isolation," *per se,* is but a manifestation of the "intolerance" which exists among the individuals of a population of territorial animals. Furthermore, isolation does not necessarily connote active defense of an area by vigorous physical combat as observed among strongly territorial animals such as birds, mammals, and fishes. Therefore, the rather even spacing of the individual male green frogs indicated that a certain degree of isolation (intolerance) existed among them.

With regard to "fixation" much variation from the topographically limited areas of most birds occurs among the vertebrates. A few examples are in order. The fresh-water fish (*Rhodeus amarus*) lays its eggs in the gills of the mussel (*Anodonta cygnaea*). In the spring the male fish becomes associated with a mussel and furiously fights other males which happen to come near. Since the mollusk moves about, the fish is associated with a constantly changing area and not with a definitely fixed one (Wunder 1933). Another example is encountered in the sexual fights of many ungulates, *e.g.,* the moose (*Alces americana*); these are not associated with spatially fixed territories. The fighting of the male moose is restricted to the vicinity of the cow or cows which move about rather freely (Hosley 1949). Then too, green frogs did not restrict their reproductive activities to spatially fixed areas. Some groups of frogs moved as far as 110 meters, meanwhile maintaining for a time their positions with regard to each other.

Even among the students of birds the matter of "fixation" is not universally accepted. In this regard the following contributions are of interest. Tinbergen (1936) suggested that the term territoriality be limited to "an area which is de-

fended by a fighting bird shortly before and during the formation of a sexual bond." But Noble (1939) pointed out that this definition would not include certain obviously territorial birds. His reference was to the European black grouse (*Lyrurus tetrix*). In this species the females merely come to the lek for breeding purposes and no persistent pairings (sexual bonds) are established. Nevertheless, the small areas immediately surrounding each courting cock have primarily the same function as the territories of other birds, *viz.*, "they make possible the male's recognition of a sexually-ready female."

The function of the organization observed within the breeding congress of green frogs is not clearly understood but the following role is suggested. The method of sex recognition in *R. clamitans* has not been studied, but very probably is similar to that in *R. sylvatica*. Banta (1914) observed in nature that a male *R. sylvatica* attempts "to mate with any frog or small moving object it encounters." Noble and Farris (1929) experimentally demonstrated that sex recognition results from this trial and error method, the males retaining "their grip on those individuals having a certain girth and degree of firmness of body." The warning croak of an embraced male possibly facilitates recognition. However, *R. sylvatica* breeds for but a short period in the spring of the year, whereas *R. clamitans* has a prolonged breeding season in which apparently only a small number of females arrive at the breeding ponds in any one part of the season. Thus when females arrive the competition among males for mates is accentuated and continues over a long period. If the continuous trial and error procedure of sex recognition were maintained throughout the entire season a tremendous expenditure of energy would occur, thus perhaps reducing the food reserves and thereby diminishing the ardor of the males. Instead, it is thought that early in the breeding season, males do aggressively test the sex of nearby males and having done so maintain the same general position with regard to these identified individuals. In this way, repetitious recognition of males is greatly reduced and the appearance of another frog in the vicinity is more readily detected. Thus, in breeding congresses of green frogs, a period of aggression is followed by one of social stability, a situation similar to that occurring among many species of other classes of vertebrates (Collias 1944). The maintenance of spatial relations, even after extensive movements over land, more conclusively indicated that a frog very probably recognizes his neighbors, and further, the rather even spacing among individuals indicates that a type of territorial behavior is present.

Even though there is no active defense of an area as is generally associated with well established territories, the green frog exhibited a type of organization which possibly serves the same function as territoriality, *viz.*, "it permits conservation of energy for reproduction" (Noble 1939). Therefore in view of the above mentioned similarities, I think that it is proper to classify the green frog as having a primitive type of territoriality.

It is interesting to speculate why a large number of males moved from the middle pond to the western one and still preserved their spatial relationships with one another. This shift in population occurred immediately before two-thirds of all the egg clusters observed in this study were found. All of these clusters were in the western pond. Thus one wonders whether the males moved to the western pond before the arrival of the females or whether the males responded (indirectly) to the presence of the females. The latter explanation is more plausible than might first be anticipated. Banta (1914) reported that the call of a clasping male of *R. sylvatica* "is somewhat modified (apparently by the contact of the male's throat with the female's body) so that one can often distinguish the call of the pairing from that of the single male." *R. clamitans* has paired internal vocal pouches similar to those of *R. sylvatica* and it is

possible that the louder calls of mating green frogs may serve as key stimuli in attracting nearby males.

Summary

As part of an extensive ecological study made near Ann Arbor, Michigan, in 1948 and 1949, a detailed study of spatial relations was made on one study area comprising two small ponds. The breeding season of these frogs was long, from about mid-May to mid-August. Most adult males spent the entire period at the breeding ponds, but females are thought to have averaged about a week there. In the breeding areas the adult males were observed to be spaced at surprisingly uniform distances of about 2–3 meters. In 1949, 148 males were captured 270 times in the breeding area. Analysis of this data showed that several of them made approximately the same movements at the same time. In addition, it was demonstrated that frogs in a cluster tended to remain in that cluster for periods of about two months in spite of the fact that the entire group made overland movements of more than 110 meters. In view of the comparatively long breeding season of green frogs, this organization would help to conserve the energies of the males and also would permit them to detect more quickly the presence of females. In any case, the data indicate that during the breeding season a small proportion of the activity range is maintained as a primitive type of territory which has certain similarities to the more strongly developed territories of other vertebrates.

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STATISTICAL ANALYSIS APPLIED TO A VEGETATION TYPE IN NEW ZEALAND

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Introduction

In New Zealand, ecological studies of communities are still mainly descriptive and based on qualitative observations. An attempt has been made in the present investigation to apply some quantitative methods, frequently used by British and American workers, to a widespread New Zealand community.

All attempts to analyze communities statistically have been based on data derived from small sample plots distributed at random within the area under investigation. These sample plots obviously do not require to be larger than is absolutely necessary, and Cain (1943) has defined the "minimal area" as "the least area upon which a community can develop its typical composition and structure." Recent workers in both the U. S. A. and Great Britain have also shown that statistical analysis is primarily of importance in showing whether individual species in a community are distributed at random or are over-dispersed. Unless distribution is at random statistical analysis applied to vegetation cannot yield an objective picture of the vegetation. In the case of tree vegetation, if the seedlings are eliminated it is often found that the adults are distributed at random. Unpublished work carried out in the Auckland department has shown that the dominant of the scrub community investigated is in fact randomly distributed.

Statistical analysis as used in this paper depends on the use of a sample plot and much of the early work was based upon a square sample plot. However, Clapham (1932), using data from quadrats on grazed dune grassland, showed that for such vegetation a rectangular plot yields more information than a square of equivalent area.

Both Arrhenius (1923) and Gleason (1925) tried to formulate mathematical expressions for the relationship between number of species and area, whilst more recently, Williams (1944, 1947) has applied the theory of the logarithmic series in order to show the relationship between number of individuals, number of species, and area.

The immediate objects of the investigation reported here were to determine:

(1) The minimal size of the sample plot.
(2) The best shape statistically for the sample plot, i.e., square or rectangle.
(3) Whether the logarithmic series could be applied with satisfactory results.

The community selected for this work was *Leptospermum* shrubland in its intermediate stage.

Leptospermum Shrubland

In New Zealand, derelict land passes through a shrub stage before reverting to climax forest. This shrub stage is dominated by *Leptospermum scoparium* and *L. ericoides* in the shade of which the forest trees develop.

Cockayne (1928) recorded that this shrubland extended throughout New Zealand. The total number of species found in the community is given as 80, of which 25 do not occur south of the Auckland district. Cockayne recognized three stages of development:

(1) Young *Leptospermum scoparium* and/or *L. ericoides* occur in such

[1] The work was carried out by the first author but the manuscript has been prepared and seen through the press by the second author under whom the work was performed.

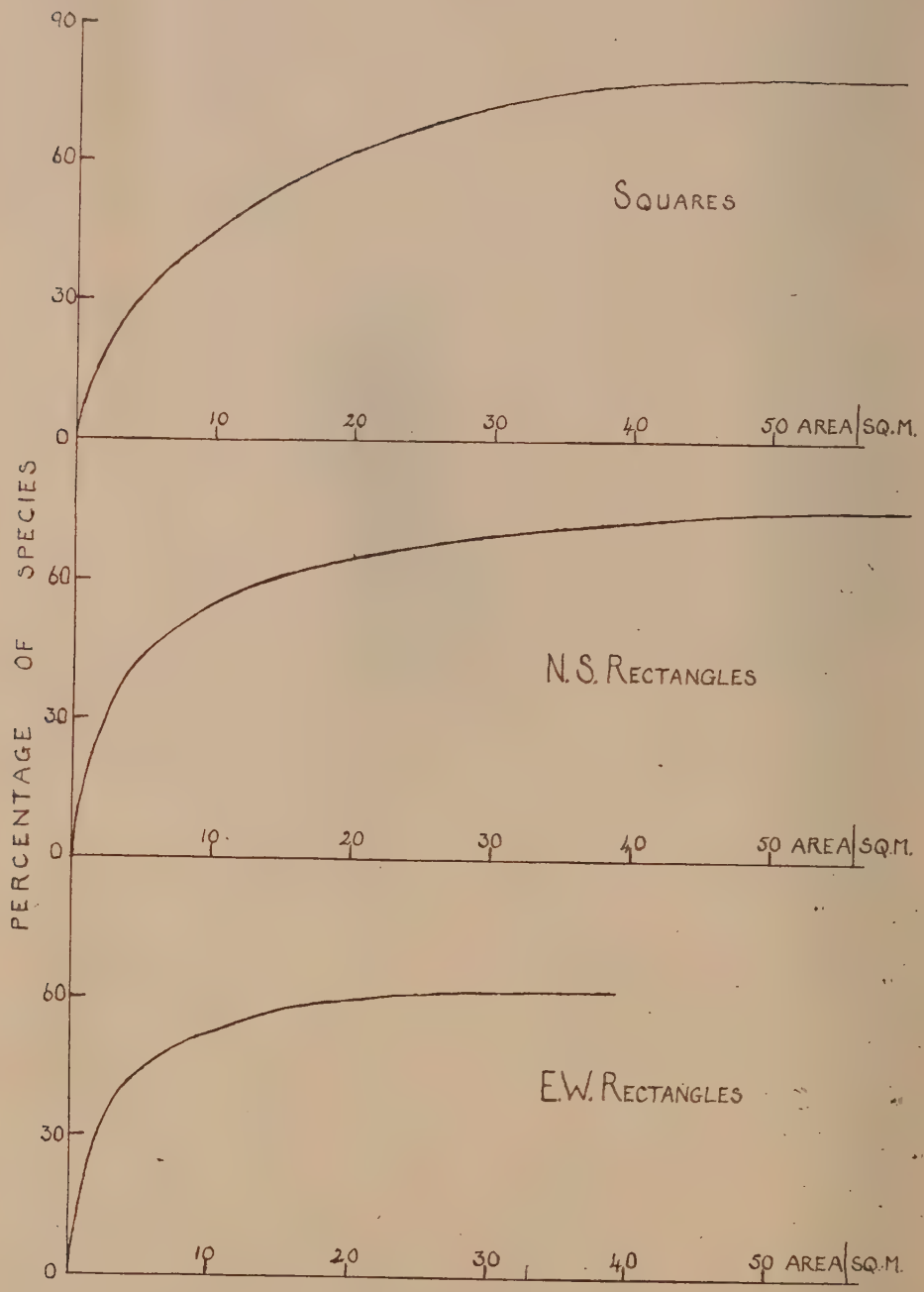

FIG. 1. Minimal area curves for squares and rectangles placed, respectively, north-south and east-west.

numbers that other species are prevented from entering, and the reduction of light intensity prevents development of an undergrowth.

(2) Many *Leptospermum* plants fail to survive, and sufficient light enters for germination of seeds of forest tree species. This is termed the intermediate stage.

(3) The forest tree species outgrow the *Leptospermum* and finally oust it. Old *Leptospermum* shrubland therefore represents the stage just prior to the subordination of the *Leptospermum*.

The data for this study were compiled on the Auckland University College reserve at Swanson, which has been described by McKinnon (1930).[2] This now contains good examples of the intermediate shrubland. In these areas, *Leptospermum scoparium* with some *L. ericoides* are the dominants, the plants varying in height from 10–15 ft. Occasionally small trees of *Agathis australis, Phyllocladus trichomanoides, Nothopanax arboreum,* and *Olearia cunninghamii* may occur in the canopy. The ground is completely covered with a dense mass of *Gleichenia microphylla* and *Schoenus tendo* with some *Lycopodium densum, Pteridium esculentum,* and *Dianella intermedia.* Beneath these are to be found seedlings of the following forest species:

Phyllocladus trichomanoides
Agathis australis
Pseudopanax crassifolium
Coprosma spp.
Dacrydium cupressinum
Leucopogon fasciculatus
Suttonia australis
Olearia cunninghamii
Geniostoma ligustrifolium
Podocarpus hallii
Podocarpus dacrydioides.

Determination of the minimal area

Minimal area curves were constructed in the usual manner using squares of increasing size and rectangles running in two directions at right angles. On inspection of the graphs obtained (Fig. 1) it was decided that squares or rectangles of 36 sq. m. represented the minimal area and all subsequent quadrats were of this size. It might be argued that this represented a slight underestimation, but it would appear that any increase in the number of species after this point would be small. Furthermore 36 sq. m. is readily resolved into a square of sides 6 m. and a rectangle 24 m. long by 1½ m. wide, based on Clapham's result that the best shape for a rectangle is one with sides of ratio 16:1. Later work (unpublished) on another problem in the same type of community has confirmed this selection of 36 sq. m.

The shape of the minimal area

Clapham (1932) compared the results obtained from square and rectangular sam-

[2] McKinnon, A. D. 1930. Unpublished B. For. Sc. thesis, Auckland.

TABLE I. *Analysis of variance of data used by Clapham (1932)*

	Sum of squares	Degrees of freedom	Mean square	Variance ratio	Probability
Squares					
Squares (16)	1.73	15	.12	.71	.20
Species (5)	6.34	4	1.59	9.35	.001
Error	10.07	60	.17		
Total	18.14	79			
Rectangles					
Rectangles (16)	1.31	15	.09	1.13	.20
Species (5)	5.11	4	1.28	16.	.001
Error	4.70	60	.08		
Total	11.12	79			

TABLE II. *Analysis of variance of data from Leptospermum shrubland*

	Sum of squares	Degrees of freedom	Mean square	Variance ratio	Probability
Squares					
Squares (8)	4.82	7	0.69	11.5	.001
Species (10)	13.21	9	1.47	24.5	.001
Error	3.85	63	0.06		
Total	21.88	79			
Rectangles					
Rectangles (8)	1.04	7	0.15	1.4	.02
Species (10)	10.59	9	1.18	10.7	.001
Error	6.83	63	0.11		
Total	18.46	79			

ple plots by estimating the variance (V) between them, using the formula

$$V = \frac{1}{n-1} \overset{n}{S}_{1} (x - \bar{x})^2,$$

where x is one of n observations the mean of which is $\bar{x}$. He found that rectangles which were 16 times as long as wide were less variable than squares of similar area in the ratio 220:401. Rectangles with sides of ratio 4:1 were also less variable, but in the ratio 349:401.

An analysis of variance for Clapham's data was made using the logarithms of his numbers, and the results are given in Table I. Consideration of the error terms for squares and rectangles confirms Clapham's conclusion that rectangles show less variation than squares.

In order to determine whether the minimal area in *Leptospermum* shrubland should take the shape of a square or a rectangle, a series of squares and rectangles was laid out and the numbers of individual species rooted within these areas were counted. Rectangles were laid out in the N.–S. direction only and eight sets of squares and rectangles were counted. The results of an analysis of variance for these data are given in Table II.

It will be noted that in this case the squares show considerably less variation than the rectangles. This is the very reverse of the results obtained by Clapham. One can only conclude that, whereas rectangles are less variable than squares of similar area in the study of grassland, nevertheless squares are less variable than rectangles of similar area in the study of a community such as *Leptospermum* shrubland. The rectangular quadrat is not therefore necessarily the best type of sample plot, and one should investigate this problem in each type of community.

The application of the logarithmic series to Leptospermum data

Williams (1944, 1947) has discussed Fisher's (1943) theory of the logarithmic series and its application to problems dealing with area, numbers of species, and number of individuals, e.g. the number of species of plants on areas of different sizes in an aspen association.

The method in outline is as follows:

The logarithmic series $x, \frac{x^2}{2}, \frac{x^3}{3}, \frac{x^4}{4}$, etc.

can be written in a more general form:

$$\frac{n_1}{x}(x), \frac{n_1}{x}\left(\frac{x^2}{2}\right), \frac{n_1}{x}\left(\frac{x^3}{3}\right), \frac{n_1}{x}\left(\frac{x^4}{4}\right), \text{ etc.}$$

$$= n_1, n_1\frac{x}{2}, n_1\frac{x^2}{3}, n_1\frac{x^3}{4} \text{ etc.}$$

where n_1 = number of groups with one unit,

$n_1\frac{x}{2}$ = number of groups with two units etc.,

x = a constant less than unity.

It has been shown in theory and practice that for all samples from the same population, the ratio n_1/x is a constant, and this ratio has been called by Fisher the "index of diversity" (α). If this value α is substituted for n_1/x in the above equation, the logarithmic series may now be written as αx, $\alpha\frac{x^2}{2}$, $\alpha\frac{x^3}{3}$, $\alpha\frac{x^4}{4}$, etc. and

S (total number of species)
$$= -\alpha \log_e (1 - x),$$

N (total number of individuals)
$$= \alpha \frac{x}{1 - x}.$$

Combining these, $S = \alpha \log_e \left(1 + \frac{N}{\alpha}\right)$.

The index of diversity may also be found if the number of species is known from two areas of different sizes. Assuming that the number of individuals is large and is proportional to the area of the samples, it can readily be shown that if one sample be p times the other and the two samples contain pN and N individuals respectively, then $S_{pN} - S_N = \alpha \log_e p$.

Now α is a function of S and N, so once α has been determined a graph may be drawn to show this relationship for that particular value of α, by plotting log N as ordinates against corresponding values of S as abscissae. Curves so obtained approximate to straight lines for higher values of log N.

If the average number of individuals per unit area (1 square m.) be y, then the total number of individuals in a sample $N = yx$ area of sample, or log N = log y + log area. For samples from the same population y will be constant and log N = log area + log constant.

Hence, if for a given population α is known, the graph of log area as ordinates against number of species as abscissae may be superimposed on the graph of α. These points may lie on a straight line

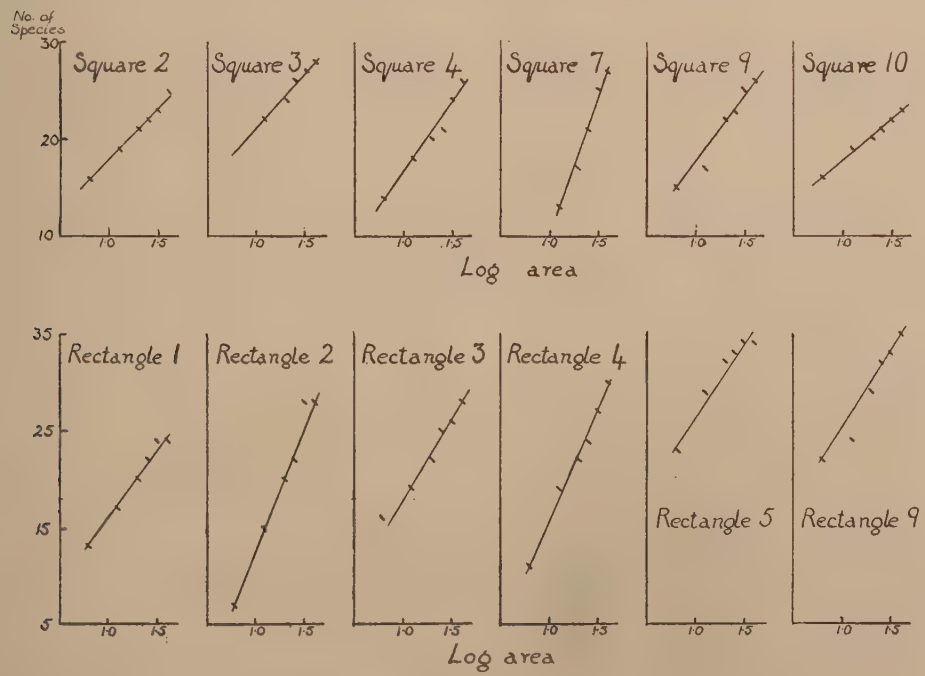

FIG. 2. Number of species—log. area curves for squares 2, 3, 4, 7, 9, 10 and rectangles 1–5 and 9.

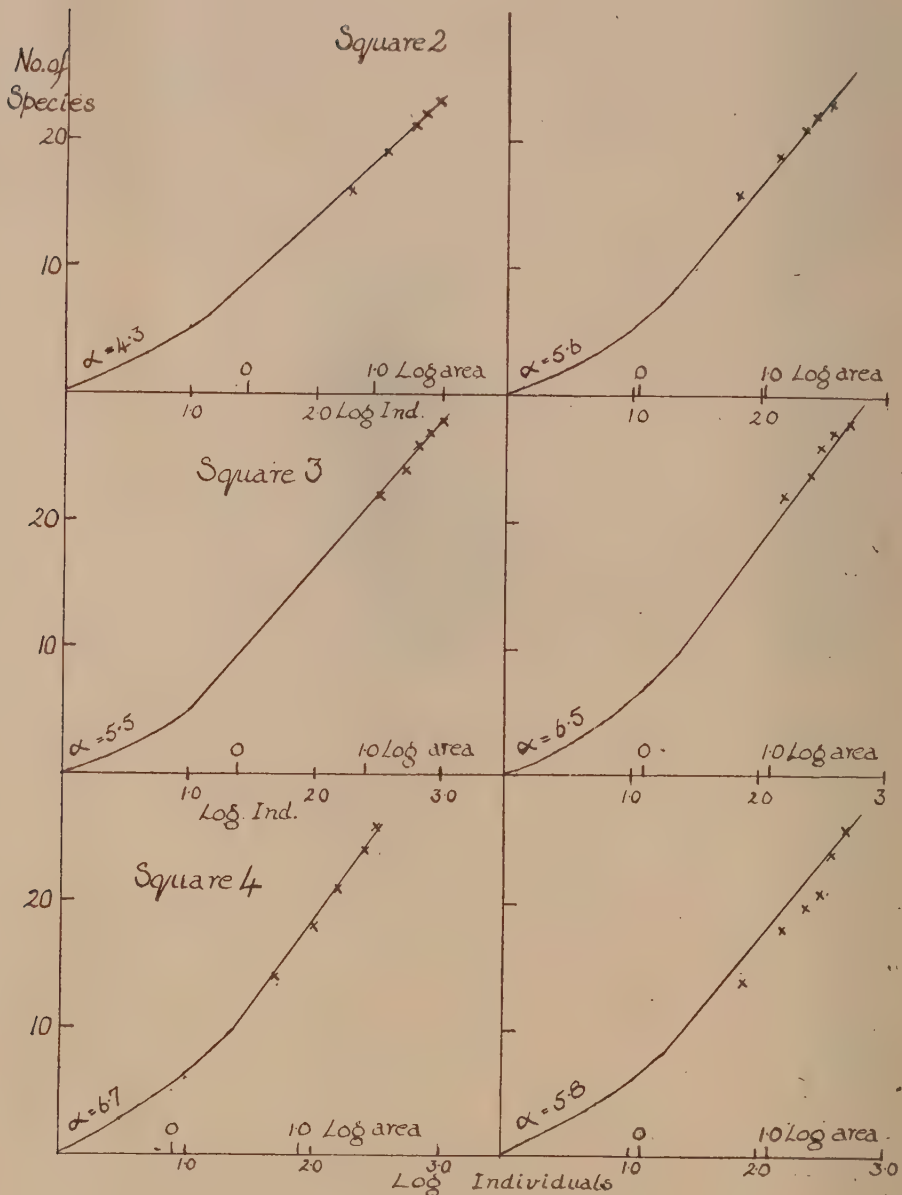

FIG. 3. Left: Number of species—log. area curves superimposed on number of species—log. number of individuals for squares 2–4. α calculated from $S_{pN} - S_N = \alpha \log_e p$. Right: Number of species—log. area curves superimposed on number of species—log. number of individuals for squares 2–4. α calculated from $S = \alpha \log_e (1 + N/\alpha)$.

and by shifting the ordinates a certain distance, these points then coincide with the line for α. The new ordinates of all these points are made up of the log value of the corresponding area plus a constant which has been selected by inspection. This constant, which is the distance through which all the points have been moved, corresponds to the log constant of the equation above and equals log y. Hence y can be found and the number of individuals in the sample calculated.

The method of collection of data for the previous work enabled α to be calculated from the equation $S_{pN} - S_N = \alpha \log_e p$, for those cases where there was a linear relationship between number of species and corresponding log area. This relationship definitely existed for squares 2, 3, 4, 7, 9, and 10 and rectangles 1, 2, 3, 4, 5, 8, 9 (Fig. 2). Squares 3, 7, and rectangles 3, 9 showed the linear relation over the range 12–36 sq. m.; rectangles 5 and 8 from 12–30 sq. m., and square 2 from 6–30 sq. m. Log number of individuals/number of species curves were constructed for the different values of α, and log area/number of species curves were superimposed on them.

By adjusting the ordinates of points from the "log area/number of species" curves, good fits to the α curves were obtained for squares 2, 3, 9, and rectangles 3, 4, 9, and reasonably good fits for squares 4, 7, 10, and rectangles 1, 2, 5, 8 (Fig. 3). Points which did not show good approximation to straight lines were not further considered.

Values for y, the number of individuals per unit area, were obtained from the graphs, and the numbers of individuals (N) to be expected on areas of 36 sq. m. could be calculated. The calculated and observed values of N are compared in Table III. It was found that in no case was there any agreement between calculated and observed figures.

The values obtained for y ranged from 2 to 509, whereas actual observations gave a range of 9–50. The values for all quadrats except two rectangles and three squares are larger than expected.

It was not possible to estimate the number of individuals of *Schoenus tendo* and *Gleichenia microphylla* which form the dense ground cover. These two species were therefore excluded from the number of species in the various samples. This has not affected the value of α, since the evaluation of α involves a difference in

TABLE III. *Values of* α *(from* $S_{pN} - S_N = \alpha \log_e p$*),* y*, calculated and observed* N*, for squares 2, 3, 4, 7, 9, 10 and rectangles 1, 2, 3, 4, 5, 8, 9*

Square	α from $S_{pN} - S_N = \alpha \log_e p$	y (for 1 sq. m.)	N for 36 sq. m. calc.	N for 36 sq. m. obs.	α from $S = \alpha \log_e\left(1 + \frac{N}{\alpha}\right)$
2	4.3	27	810*	379	5.6
3	5.5	25	900	497	6.5
4	6.7	8	288	491	5.8
7	12.8	2	72	415	6.3
9	6.1	25	900	1,110	6.0
10	3.9	501	18,036	1,366	6.2
Rectangle	α from $S_{pN} - S_N = \alpha \log_e p$	y	N for 36 sq. m. calc.	N for 36 sq. m. obs.	α from $S = \alpha \log_e\left(1 + \frac{N}{\alpha}\right)$
1	6.1	8	288	760	4.7
2	11.7	3	108	553	6.2
3	10.0	4	144	660	6.0
4	10.6	4	144	471	6.9
5	6.8	32	960*	604	7.8
8	6.2	32	960*	735	6.8
9	10.0	8	288	1,421	6.5

* N (calculated and observed for 30 sq. m.).

TABLE IV. *Calculated and observed values of n_1 the number of species with one individual, using: (A) α from $S_{pN} - S_N = \alpha \log_e p$, (B) α from $S = \alpha \log_e \left(1 + \frac{N}{\alpha}\right)$*

	(A) Calc. n_1 on 36 sq. m.	(B) Calc. n_1 on 36 sq. m.	Obs. n_1 on 36 sq. m.
Square			
2	4.3*	5.5	5
3	5.4	6.4	3
4	6.6	5.7	4
7	12.4	6.2	8
9	6.1	6.0	3
10	3.9	6.2	5
Rectangle			
1	6.1	4.7	1
2	11.5	6.1	5
3	9.8	5.9	4
4	10.4	6.8	7
5	6.7*	7.7	8
8	6.1*	6.7	5
9	9.9	6.5	5

* n_1 (calculated and observed) for 30 sq. m.

number of species between two areas when the species concerned are present on both. The effect has been to decrease y and hence the calculated number of individuals. However, the observed numbers of individuals include no figures for the above two species, so the two sets of figures may legitimately be compared.

Williams (1944) notes that he found an inconsistency throughout his work, viz., that the observed values of n, the number of groups with one unit, were greater than calculated.

Although n_1 has not entered into the above calculations, it can be found as follows:

$$x = \frac{N}{N + \alpha}$$

$$\left(\text{a transformation of } N = \alpha \frac{x}{1 - x}\right)^{3}$$

and since $n_1 = \alpha x$, the above expression can be inserted in place of x.

[3] $\alpha x = N(1 - x)$

$\alpha x = N - Nx$ or $\alpha x + Nx = N$

$$x = \frac{N}{N + \alpha}.$$

The observed and calculated values of n_1 are shown in Table IV. In 10 cases out of 13 the calculated n_1 is above the observed, whilst in the other 3 cases the observed figures are greater than the calculated.

Now α was calculated from the equation

$$S_{pN} - S_N = \alpha \log_e p.$$

The use of this equation involves assumptions which appear to have been justified except in two cases:

(1) The values of N are large;
(2) If the observed values of N are plotted against the area it is found that they are approximately proportional to the corresponding areas except for rectangles 5 and 8 over the smaller areas.

If both S and N are known, α can be found from the equation $S = \alpha \log_e (1 + N/\alpha)$ using tables prepared by Fisher (Williams 1947). The values of α obtained by this method are given in Table III and differ considerably from those already obtained.

When the graphs were redrawn (Fig. 3, right) using these new values of α, it was found that the log values of y, for the points corresponding to the values of S and N from which α had been derived, in many cases did not give a good fit to the α curves for the other points, that is, y led to an accurate estimate of N only for that area considered in the evaluation of α (36 sq. m.). The figures for p, the probability (Table V) indicate that even for these values of α, the calculated numbers of individuals may still show significant deviation from the observed.

If the values of n_1 calculated using the new values of α are now compared with the observed, it is still found that in 10 cases out of 13 the calculated values are greater than the observed figures, while in the remaining 3 cases they are less.

The application of the logarithmic series to work of this kind takes no account of

TABLE V. *Values of α from $S = \alpha \log_e\left(1 + \frac{N}{\alpha}\right)$ and corresponding values of y, and of N (calculated and observed), with p, the probability*

Square	α	y	N for 36 sq. m. calc.	N for 36 sq. m. obs.	P
2	5.6	11	330*	379	0.001–0.01
3	6.5	13	468	496	0.10 –0.20
4	5.8	13	468	492	0.20 –0.30
7	6.3	11	396	415	0.30 –0.50
9	6.0	28	1,008	1,110	0.001–0.01
10	6.2	32	1,152	1,366	0.0001
Rectangle	α	y	N for 36 sq. m. calc.	N for 36 sq. m. obs.	P
1	4.7	20	720	760	0.10–0.20
2	6.2	14	504	553	0.02–0.05
3	6.0	17	612	660	0.02–0.05
4	6.9	13	468	471	0.80–0.90
5	7.8	20	600	604	0.80–0.90
8	6.8	20	600*	735	0.001
9	6.5	40	1,440*	1,421	0.50–0.70

* N (calculated and observed) for 30 sq. m.

ecological factors at work within the community. If there were a general tendency for this theory to either over- or underestimate the number of individuals, the cause might be ascribed to some particular factor or combination of factors. As there is no such general tendency, it is difficult to name the factor responsible for the variations obtained.

COMPARISON OF LEPTOSPERMUM COMMUNITIES FROM DIFFERENT LOCALITIES

Williams (1944, 1947) has discussed a further application of the index of diversity (α), to a comparison of the degree of relationship of different areas. It consists in finding the number of species common to two areas of different sizes, assuming the density of the species is the same for both.

If the areas be A and B, with a and b species, respectively, and if x be the total number of different species found on A and B, then by adding B to A, increase in number of species,

$$x - a = \alpha_1 \log_e \frac{A + B}{A}$$

and similarly by adding A to B, increase in number of species

$$x - b = \alpha_2 \log_e \frac{A + B}{B}.$$

Hence

$$\frac{x - a}{x - b} = \frac{\alpha_1 \log_e \frac{A + B}{A}}{\alpha_2 \log_e \frac{A + B}{B}} = \log \frac{B}{A}.$$

Thus x can be found. Then the calculated number of species common to $A + B = (a + b) - x$ and the *observed* number of species common to both expressed as a percentage of the calculated gives an indication of the degree of relationship.

In this study samples 1–8 at Swanson were compared:

(a) with 2 areas (36 sq. m. each) in late intermediate *Leptospermum* scrubland at Oratia (another College property).
(b) with samples 9 and 10 in another part of the Swanson property but in the same type of community as samples 1–8.

Using the above equation, the data for substitution are:

(a) Oratia	A = 72 sq. m.	a = 48 species.
Swanson 1–8	B = 576 sq. m.	b = 52 species.
(b) Swanson 9–10	A = 144 sq. m.	a = 53 species.
Swanson 1–8	B = 576 sq. m.	b = 52 species.

The values of x that were obtained showed that for (a) the calculated number of common species was 90. The observed field number was 33 = 37% of the calculated number. For (b) the calculated number of species common to both was 46. The observed number was 41 = 89% of the calculated.

On Williams' theory therefore there is a high degree of relationship between the two Swanson areas but only a slight degree between Oratia and Swanson.

These results may have no real meaning because the sample areas at Swanson did not conform satisfactorily to the logarithmic series (see previous section), upon the use of which the present theory is based.

Although only 33 species are common to both Oratia and Swanson, nevertheless they are those typical of the intermediate *Leptospermum* community; the remaining species mostly form the ground vegetation. On this basis Oratia and Swanson 1–8 are similar. The same is also true of the two Swanson regions.

So far, the actual numbers of individuals have not been considered. For Oratia and Swanson the graphs (Fig. 4) of the percentage number of individuals of the ten commonest species show no similarity. Only two of these species, *Agathis australis* and *Phyllocladus trichomanoides* are important in the next stage of the succession. Any decision as to degree of relationships between seral communities of this type should be largely influenced by the presence or absence of the future dominants. On this basis Oratia and Swanson are clearly closely related.

Although it would seem that the two Swanson regions are similar, nevertheless when the percentage number of individuals of the same 10 species are considered there

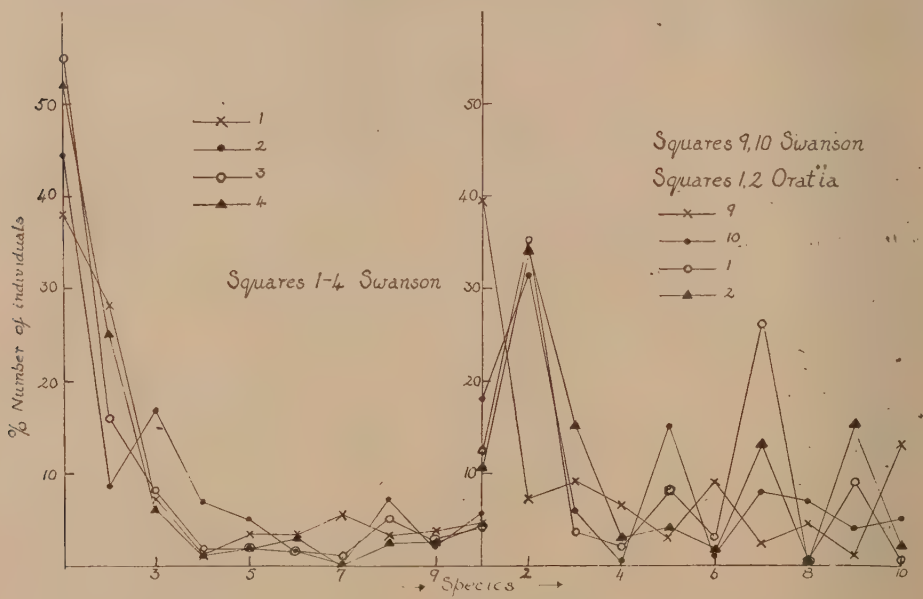

FIG. 4. Percentage number of individuals—species curves for squares 1–4 Swanson (left), squares 9, 10 Swanson (in a different area) and squares 1, 2 Oratia (right).

is a very clear difference between Swanson 1–8 and 9–10; and these differences are likely to be observed at the next stage in the succession.

Summary

1. The minimal area of a sample plot for the intermediate *Leptospermum* community is 36 sq. meter.

2. An analysis of variance gives the result that squares are less variable than rectangles.

3. The fact that "the number of species/log area" curves give good fits to the α lines, when α is derived from the equation

$$S_{pN} - S_N = \alpha \log_e p$$

is no indication that reliable estimates for N will be obtained. As the value of the use of the theory of the logarithmic series and index of diversity for this work lies in the fact that it should be possible to deduce the number of individuals having counted only the number of species, one is forced to conclude that the theory has no practical application to *Leptospermum* vegetation, and perhaps to other similar vegetation.

4. In any plant community there are so many variable factors governing and determining the existence of that community that it seems doubtful whether any mathematical expression could be formulated which would take into account all these factors.

Our thanks are due to Dr. E. J. Godley for his invaluable assistance with the preparation of the data, to Mr. H. Thomson, and to those friends who assisted with the practical work.

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NOTES AND COMMENT

AMOUNTS OF BIG SAGEBRUSH IN PLANT COMMUNITIES NEAR TENSLEEP, WYOMING, AS AFFECTED BY GRAZING TREATMENT

Current range vegetation is more often than not a product of varying degrees of past disturbance by man's livestock. Grazing disclimaxes occur over such vast areas, and are of such long standing, that many stockmen do not realize their ranges once did and can again produce a quite different kind of vegetation. This seems particularly true in the Big Horn Basin of Wyoming where the characteristic form and color of big sagebrush (*Artemisia tridentata* Nutt.) dominates the landscape of foothills and lower mountains. Here, most stockmen consider big sagebrush as a naturally dominant component of their native pastures or ranges.

Weaver and Clements (1938: 533–534) considered the sage brush climax as being confined essentially to the central portion of the Great Basin. In many other areas of the intermountain region, well-established stands of big sagebrush have been found to deter the establishment of adapted grasses (Robertson 1947). For that and other reasons, methods of burning (Pechanec and Stewart 1944) as well as many kinds of mechanical devices and chemical treatments, have been used to eradicate big sagebrush in preparation for reseeding or to hasten natural reestablishment of desirable native forage species.

Since natural plant succession aids in restoration of a type of vegetation in balance with climate and soil, it is important for the rancher and technician alike to know the end product or climax for each range site when secondary succession is encouraged.

The primary purpose of this paper, therefore, is to report successional trends under different grazing treatments, especially as related to relative amounts of big sagebrush in certain plant communities. A secondary purpose is to report response in relative coverage by climax grasses under these same grazing treatments.

Location

Four native pastures located 2 to 5 miles south of Tensleep, Wyoming, were selected for study. They are within a short distance of each other on the same ancient terrace above the Nowood River. They were selected because of strictly comparable soil, slope, exposure, and precipitation. The soils of the pastures belong to the group with light brown topsoils as classified by Thorp (1931) who made a preliminary study of relations between climates, soils, and vegetation in the area.

The elevation of the pastures is between 4,200 and 4,300 feet above sea level. The average annual precipitation recorded at Tensleep, Wyoming, is 10.43 inches. A maximum of 15.87 inches was recorded in 1937 and a minimum of 1.2 inches was recorded in 1900. Approximately 48 per cent falls during the growing season. The average annual precipitation during the 8 years of this study was slightly above the half-century average. Temperatures vary from −42° F to 106° F with a mean annual temperature of 43° F. The average date of the last killing frost is May 15 and the average date of the first killing frost is September 15.

Procedure

A study of the vegetation on 4 neighboring pastures under different ownerships was begun in 1942. Originally, the point-observation-plot method described by Stewart and Hutchings (1936) was used to determine species composition. In subsequent years, plans of range management were developed with the owner-operators in cooperation with the Nowood Soil Conservation District. In the course of providing technical assistance to the District's cooperators, the author observed each pasture at least once each year. The statements of the operators as to seasons and numbers grazed, though not exact, were considered adequate for the purpose of this study.

In August, 1949, the range condition of each of the 4 pastures was evaluated according to the method developed and described by Dyksterhuis (1948, 1949).

Results

The vegetation of the 4 pastures was quite similar in 1942. Big sagebrush was dominant in all pastures and grasses were clearly subordinate. Amounts of each are given later in relation to amounts occurring in 1949. By 1949, the pastures showed great differences in species composition. These differences could be attributed only to differences in seasons of use and degrees of grazing over the 8 year period. Figure 1 shows the pastures as they appeared in August, 1949.

In Figure 1, the pasture labeled D shows essentially the appearance of all 4 pastures in 1942. Pasture A was rested (deferred) throughout the growing season 4 times between 1942 and 1949. In those years, however, it was utilized fully after the growing season ended. In the other 4 years, it was used moderately during the growing season.

Pasture B was rested during the growing

season 3 times between 1944 and 1949. In 1947, the kind of livestock grazed was changed from sheep to cattle and the stocking rate reduced.

In Pasture C the stocking rate was reduced in 1945 and the pasture was rested throughout the growing season twice between 1945 and 1949.

In Pasture D there was no significant change in stocking rate or system of management from 1942 to 1949.

The 8 years of slightly above normal precipitation had no evident effect on relative coverage by species in Pasture D. Therefore, changes in the vegetation of the others may be attributed to differences in management.

Figure 2 shows species composition, or relative coverage, by major species in each of the 4 pastures in 1949.

The 4 pastures referred to as A, B, C, and D in Figure 2 were arranged in that order because of obviously greater departure from climax vegetation in the order A to D. Wright and Wright (1948), after a study of many areas of relict vegetation in south central Montana observed that the result of overgrazing had been loss in vigor and density of native grasses which permitted *Artemisia tridentata* to predominate. In this study, the evidence seems equally clear that proper management of grazing has permitted the grasses to reduce big sagebrush to a subordinate role in the community. In 1942, bluebunch wheatgrass (*Agropyron spicatum* (Pursh) Scribn. and Smith) and western wheatgrass (*Agropyron smithii* Rydb.) together made up no more than 25 per cent of total coverage in any of the pastures while big sagebrush made up 50 to 55 per cent in each. By 1949, as shown in Figure 2, big sagebrush had been reduced to 10 per cent in A and 15 per cent in B while the two grasses had increased to 75 per cent in A and 65 per cent in B. Meanwhile, relative coverage in Pasture D remained essentially unchanged.

Areas selected to be representative of pastures A and D were clipped in September of 1949. Only the current year's growth of sagebrush was taken. The clippings indicated an air-dry yield of 1640 pounds per acre from Pasture A of which 160 pounds was big sagebrush and a yield of 820 pounds per acre from Pasture D of which 600 pounds was big sagebrush. Pasture D had been grazed prior to September but the yield of sagebrush was nonetheless about 4 times greater.

Species making up 5 per cent or less of the total coverage are not included in Figure 2.

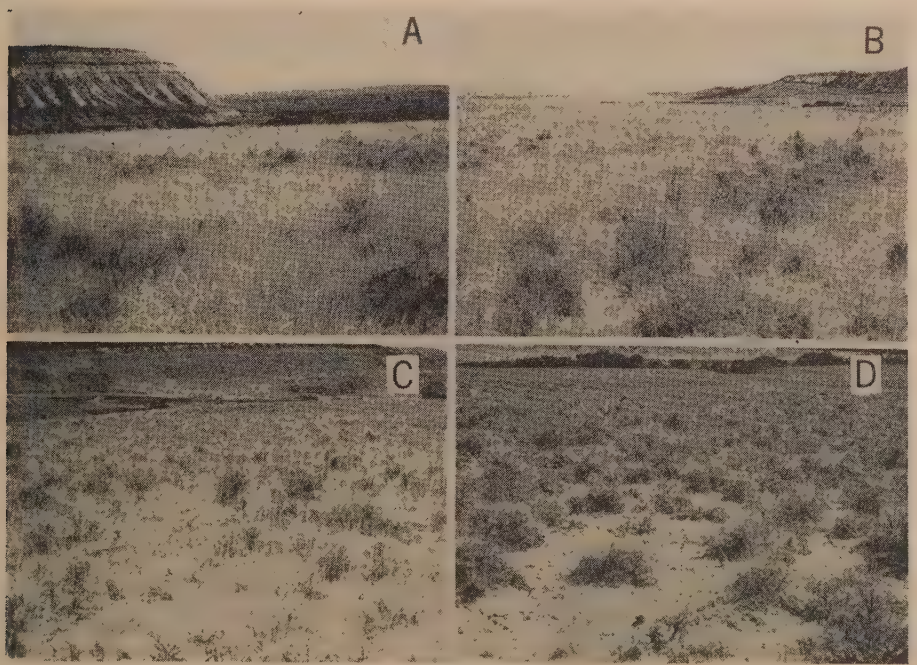

FIG. 1. Four pastures near Tensleep, Wyoming, as they appeared in August, 1949. All pastures resembled D in appearance in 1942. Dead stems of big sagebrush are common under the grass of pastures A and B. Seedlings of big sagebrush are common in pasture D.

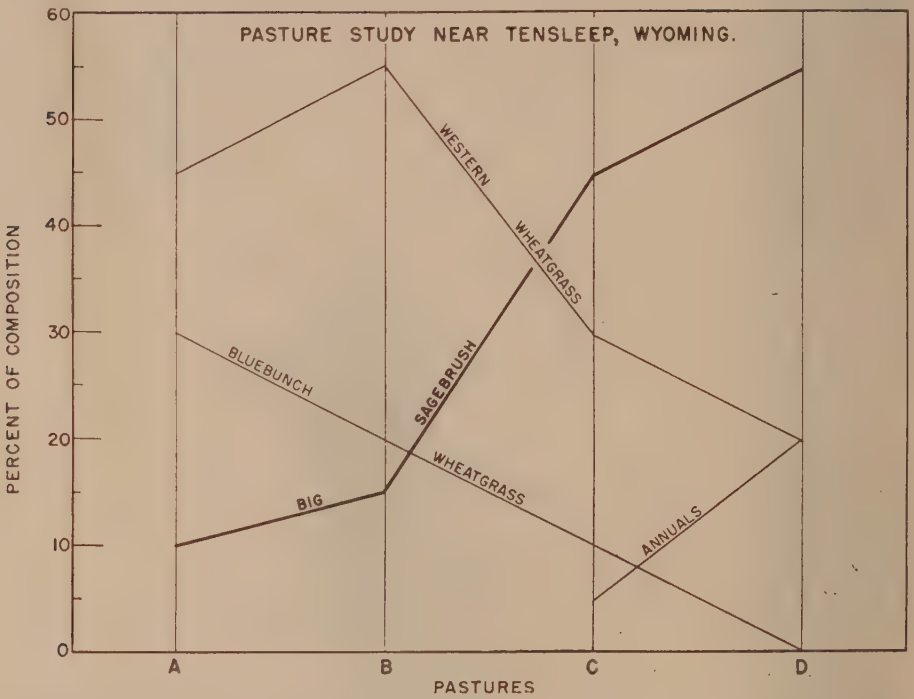

FIG. 2. Graph showing per cent of total coverage by major species on 4 pastures in 1949 after 8 years of different grazing treatments. The pastures occur on a uniform site and in 1942 all had a species composition similar to that of D.

FIG. 3. A fence line contrast near Tensleep, Wyoming. Dominance of big sagebrush on the one side and native grasses on the other resulted from two different systems of management.

Among these in Pastures A and B, were perennials, especially, needleandthread (*Stipa comata* Trin. and Rupr.), prairie Junegrass (*Koeleria cristata* (L.) Pers)., and Sandberg bluegrass (*Poa secunda* Presl.). In Pastures C and D, perennials noted were Sandberg bluegrass, broom snakeweed (*Gutierrezia sarothrae* Britt. and Rusby), plains pricklypear (*Opuntia polyacantha* Haw.), and curlycup gumweed (*Grindelia squarrosa* (Pursh) Dunal).

The annuals in C and D were principally cheatgrass brome (*Bromus tectorum* L.), Japanese brome (*Bromus japonicus* Thunb.), and Russian thistle (*Salsola kali tenuifolia* G. F. W. Mey.).

Figure 3 shows two pastures near Tensleep, Wyoming. It can be reasonably assumed that climatic and edaphic factors were originally the same on each side of the fence. Therefore, the dominance of big sagebrush in the one pasture and the dominance of native grasses in the other may be attributed to differences in management applied to the two pastures.

Conclusions and Summary

1. On the area studied, big sagebrush is a dominant in a disclimax which is largely the result of past grazing practices.

2. Species of natural grazing lands in this area can be grouped according to their behavior under close grazing as decreasers, increasers, and invaders and their relative amounts used as a quantitative measure of departure from climax as reported by Dyksterhuis (1948, 1949).

3. Relative amounts of big sagebrush in excess of 10 per cent of total coverage indicated ecological degeneration.

4. Increase in relative amount of bluebunch wheatgrass afforded a measure of secondary succession on the site studied.

5. When conservative grazing and occasional resting (deferring) of pastures is practiced on this site, climax grasses can largely replace big sagebrush without artificial aid.

6. Under favorable weather and grazing conditions, climax grasses can displace big sagebrush on this site within a decade or less.

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CONCERNING THE FLOTATION MECHANISM OF NOCTILUCA

The abundance of *Noctiluca miliaris* Suriray in the vicinity of many marine biological stations has made it a frequent object of study. The single species of the genus has many peculiarities, not the least of which is its ability to float at the surface of the sea water in which it is living. Its specific gravity has been tested by several authors, using various techniques. Thus, Goethard and Heinsius (1892), as reported by Krogh (1939), found that specimens taken from sea water with a specific gravity of 1.024 would neither sink nor rise in sea water that had been diluted to a specific gravity of 1.014. Nozawa (1943) calculated from the rate of rise of the cells through water of known specific gravity that *Noctiluca* had a specific gravity of 1.0184 when the sea water was 1.0255. By direct measurement with a pycnometer, Iida and Iwata (1943) found that expressed cell sap had a specific gravity of 1.0202 when taken from animals living in sea water with a specific gravity of 1.0248, and 1.0153 when from water of 1.0193. It can be seen that the specific gravity differences between *Noctiluca* and the environmental sea water were estimated as 0.010 (Goethard and Heinsius), 0.0071 (Nozawa) and 0.0046 or 0.0040 (Iida and Iwata).

It was suggested very early by Massart (1893) that the flotation mechanism of *Noctiluca* consisted of the numerous fat droplets often found imbedded in the cytoplasm. This hy-

pothesis is not accepted by modern authors, because it has been shown that (*a*) specimens with little or no fat float just as readily as those with much (Pratje 1921), (*b*) specimens irritated by an electrical stimulus lose their vacuolar contents by shrinking, and they then sink (Lund and Logan 1925), and (*c*) the cytoplasm and the membranes by themselves will sink (Ludwig 1928). Furthermore, Rosenfeld (1904) has shown that the fat content of *Noctiluca* is in the neighborhood of 0.67 per cent, which is insufficient to account for the floating power that has been observed.

On the other hand, modern authors do not agree as to the mechanism involved. Harvey (1917), without offering any supporting data, concluded that ". . . their lower specific gravity must be due to the fact that their salt content is less than that of sea water." This hypotonicity hypothesis was supported by Ludwig (1928) on the basis of Pratje's (1921) observations that there was a relatively small solid residue after the desiccation of *Noctiluca*. Other authors, however (Goethard and Heinsius 1892; Nozawa 1943; Iida and Iwata 1943, among others), have shown conclusively that *Noctiluca* is isotonic with the surrounding medium, for it acts, within certain limits, as a simple osmometer when placed in sea water samples of differing concentrations.

Goethard and Heinsius (1892) thought that the low specific gravity must be caused by the presence of relatively large quantities of some salt with a lower specific gravity than NaCl, and in considering the possibilities they found that the only ones likely would be ammonium salts, probably NH_4Cl. They obtained a positive test for ammonia with Nessler reagent, but were not able to obtain crystals of $(NH_4)_2PtCl_6$ (Krogh 1939). Their conclusion was supported by Krogh (1939), who stated (albeit with the modification that further investigation would be of interest): ". . . the main problem can be taken as solved . . ." Krogh was followed by Prosser *et al.* (1950).

On the other hand, Iida and Iwata (1943), the latest authors to publish on this problem, succeeded in obtaining large volumes of cell sap, and they found only 0.0013 M NH_3. Even this figure probably was high, for it was obtained six hours after expression of the sap, and the authors had pointed out that "The ammonia content of the sap showed a tendency to increase spontaneously on standing."

If we accept the results of Iida and Iwata, who used more modern techniques on larger samples than did the older authors, then we can only agree with them that NH_4Cl cannot be the flotation mechanism for *Noctiluca*. These authors showed that $SO_4^=$ was low in the cell sap compared to sea water, and they calculated that if the $SO_4^=$ were replaced by Cl^- this could account for a great deal of the buoyancy. Similar low concentations of $SO_4^=$, Mg^{++} and Ca^{++} were detected by Osterhout and Dorcas (1925) in the green algae *Valonia* and *Halicystis*, and these authors calculated that the low specific gravity of *Halicystis* must be due to this fact. Gross and Zeuthen (1948) observed that certain living, active planktonic diatoms had approximately the same specific gravity as the sea water in which they lived, whereas their protoplasm and cell walls alone (as shown by sinking of dead and unhealthy individuals, as well as of resting spores) had a specific gravity considerably greater than that of sea water. Thus it was obvious that the cell sap of the diatoms had a lower specific gravity than the environmental water. The authors made no chemical analyses of diatom cell sap, but thought it likely that the low specific gravity was caused by a mechanism similar to that of *Halicystis*.

Gross and Zeuthen (1948) referred to the low $SO_4^=$ detected in *Noctiluca* cell sap by Goethard and Heinsius (1892), and concluded that this, rather than high NH_4^+ might be the cause of the low specific gravity of *Noctiluca* cell sap. On the other hand, as Cole (1940) and others have shown, low $SO_4^=$ is by no means an unusual phenomenon in the body fluids of marine animals, but occurs in many forms which have no great buoyancy.

According to Dittmar's calculations (Sverdrup, Johnson, and Fleming, 1946, p. 166), the $SO_4^=$ constitutes 7.68 per cent of the total solids in sea water. In the sample they identified as VIII '41, Iida and Iwata measured 2.51 g. of total solids per 100 g. of *Noctiluca* cell sap. Thus, if we assume the $SO_4^=$ to be present in the cell sap in the same proportion as in sea water there would be 0.193 g. of $SO_4^=$ per 100 g. of the sap, and this is equivalent to 0.285 g. Na_2SO_4 per 100 g. of sap. The specific gravity of a solution of Na_2SO_4 of this strength would be approximately 1.0021. Now if all this Na_2SO_4 were replaced by an equivalent amount of NaCl, the latter would amount to 0.235 g. of NaCl per 100 g. of sap. The specific gravity of such a strength of NaCl solution would be 1.0012. Thus the difference of specific gravity caused by the substitution of NaCl for Na_2SO_4 would be only 0.0009, whereas the observed difference between the specific gravity of the cell sap and of the sea water for the sample under consideration was 0.0040. Thus the buoyancy caused would amount to less than ¼ of the observed difference. It is true that Iida and Iwata only state that "the low content of sulfate ions constitutes at least one of the chief causes for the low specific gravity."

The first author to mention the acidity of the cell sap of *Noctiluca* was Harvey (1917), who simply mentioned it in passing. Gross (1934)

tested living specimens with indicators, and came to the conclusion that the pH of the sap was in the neighborhood of 3. These observations were corroborated by Iida and Iwata (1943), who tested the freshly-expressed cell sap, and found pH values of 4.05–4.7 using colorimetric methods, and values of 4.62–4.65 using an antimony electrode. It was Gross's idea that the unusually high acidity of the cell sap constituted the flotation mechanism, though he failed to explain how it could do so. Subsequently, the same author (Gross and Zeuthen 1948), on the basis of the results of the tests on *Valonia* and *Halicystis* described above, changed his opinion on this matter. Little attention has been paid to this hypothesis. Krogh (1939) utilized Gross's observations to bolster his argument that NH_4Cl was the flotation mechanism, for at the low pH values the ammonia would appear as NH_4^+, whereas at higher pH values it would occur as the readily diffusible NH_3, in which form it would be lost to the cell.

It is one of the major purposes of the present paper to elaborate upon the acidity hypothesis of *Noctiluca* flotation. The hypothesis cannot be further confirmed or denied until additional thorough chemical analyses of *Noctiluca* cell sap have been performed.

We can readily see, by making a few simple calculations, that the substitution of H for Na and K could account both for the highly acid nature of the cell sap, and for its low specific gravity. The calculations are made using Iida and Iwata's observations on their sample VIII '41, inasmuch as these observations are more complete than the others. The Cl^- in the sea water was 0.406 M = 1.441 per cent. If for simplicity we consider 96.53 per cent of this to be NaCl and 3.47 per cent to be KCl (this is according to the proportions of Na and K in the ocean), then there would be 2.294 g. of NaCl per 100 g. of sea water, and 0.105 g. of KCl per 100 g. of sea water. The specific gravity caused by the NaCl would be approximately 0.0167 above that of pure water, and that caused by the KCl would be approximately 0.0005 above. Thus the specific gravity caused by the two salts together would be approximately 1.0172. If all of this Na and K were replaced by H, there would be 1.482 g. of HCl per 100 g. of sea water, and the specific gravity of such a solution would be approximately 1.0056. The difference between the specific gravity of the NaCl–KCl mixture and that of the HCl solution would be 0.0116. The observed difference between the specific gravity of the sea water and that of the cell sap of *Noctiluca* for sample VIII '41 was 0.0040, and thus the calculated difference would be nearly three times as much as necessary.

If only 40/116 of the Na and K were replaced by H, the calculated difference would be the same as that observed. This would make an HCl solution in the cell sap that was 0.140 N. In distilled water this much HCl would have a pH value much lower than that observed by any authors in *Noctiluca* cell sap, but with the buffering action caused by the other salts in solution in the vacuoles, the extreme pH values would be modified in the direction of neutrality. The buffering action of sea water is known, but that of the cell sap of *Noctiluca* has not been studied. It may differ so widely from that of sea water that calculations based on the latter would not be of very great value. A solution equivalent to 0.140 N HCl added to sea water would lower the pH value somewhat below the values observed for *Noctiluca* cell sap.

There is, of course, no reason why an animal should adopt only a single method of flotation at a time. It is possible that the actual specific gravity of *Noctiluca* is caused by a combination of factors. Among these we should consider the acidity, low sulfate, fat content, and possibly, if further analyses should show Iida and Iwata's data on the NH_3 content of cell sap to be misleading, the NH_4Cl content. Only further investigations along the lines initiated by Iida and Iwata can fully settle the questions that arise.

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COAST REDWOODS AND FOG DRIP

Fog drip as an important means of supplying moisture to coast redwoods (*Sequoia sempervirens* (D. Don.) Endl.) during the virtually rainless summer of their region has been imputed either directly or indirectly by many ecologists. For example, Daubenmire (1947) categorically states it; Kittredge (1948), in the opening paragraph of his chapter on fog drip gives the coast redwood as an example of a fog-belt tree, but makes no further reference to it in this sense. A number of writers relate the tree to the fog belt but leave the implications to the reader, without coming to grips with the problem. (See, for example, Jepson 1910).

These ideas perhaps are traceable to W. A. Cannon's 1901 article "Relation of Redwoods and Fog." A later study by Cooper (1917) demonstrated the problem in a more modest way, implying that fog drip is only an added factor in certain locations. But the more striking situations appear to have attracted most writers.

Those who have spent a great deal of time in these forests find it difficult to recall examples of fog drip in the better stands of redwood during the summer dry season. Since the best growths are in the coastal valleys or river flats, this is entirely in agreement with meteorological data. The California summer coastal fog has a confusing name, since in the strictest sense it usually is not a fog at all, but a stratus cloud layer. A fog is a cloud on the ground, and since Californians live in a hilly or mountainous region which takes them in and out of the cloud layer as they go up or down, they experience it as fog and give it that name—or "high fog."

The fog or stratus has been described in the meteorological literature by Blake (1928), Byers (1930, 1931, 1944), Neiburger (1944), Petterssen (1936), Vernon (1936), and others. The data show that the cloud layer is generally not below 300 feet, more commonly with the base at 800 to 1,200 feet in the coastal valleys. The top usually is between 1,000 and 3,000 feet, with an average at about 1,500 feet. At the ocean or cliffs, the cloud may be somewhat lower and fogs sometimes occur immediately on the ocean surface. At some localities these surface fogs seem to form when the coast valleys, where the redwoods grow, are mostly clear. Around Monterey Bay they often reach such trees as the Monterey cypress (*Cupressus macrocarpa* Gord.) and Monterey pine (*Pinus radiata* Don.) but seldom reach the major redwood groves. Redwoods, or at least healthy specimens of them, do not grow in such exposed places.

The effect of the so-called fog belt is to be found in factors other than fog drip. They are those associated with reduced evapotranspiration, namely, 1) reduction of the number of hours of sunshine and 2) reduction of daytime temperature. In the coastal valleys the stratus, in a typical situation, dissipates at about 10 A.M., standard time, during the summer days and forms or moves in after sunset. In the sunny afternoons the sea breeze increases as the ocean-land temperature contrast reaches its maximum, thus providing an automatic air-conditioning action. The quantity of water vapor in the air remains constant, corresponding to a dew-point temperature of about 50 to 55° F, so the relative humidity varies inversely with the dry-bulb temperature, and runs from near 100 per cent in the early morning to about 60 per cent in midafternoon. On nights when the stratus does not reach into the valleys, dew is likely to condense out of the moist air to the radiation-cooled earth. Although apparently very small in amount, this dew is

more important than fog drip in valley locations in summer.

In regions such as the Santa Cruz mountains where some of the finest redwood groves are found in the valleys, the slopes have Douglas fir trees or, in drier locations, grasses, chaparral and live oaks. Fog drip reaches the Douglas firs and other slope trees, but the redwoods grow below. Only a few redwoods find a suitable footing in the elevated swales where summer "fog" may reach them. Professor C. E. Olmsted has suggested to the author that the relative distribution of the Douglas fir and redwoods is the same as that found farther north between Douglas fir and arborvitae, western hemlock, Sitka spruce.

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ANTAGONISM BETWEEN DIFFERENT SPECIES OF HYDROIDS ON THE SAME SHELL

On July 6, 1952, while seasonally employed at the Prince Edward Island Biological Station of the Fisheries Research Board of Canada, the writer obtained a living hermit crab, *Pagurus* sp., in a shell of *Polinices heros* from about six feet of water at the mouth of Malpeque Bay, P. E. I. The exterior of the shell was nearly covered by two colonies of hydroids of different species; one of these was *Hydractinia echinata,* and the other probably *Podocoryne carnea.* The identification of the latter species is slightly uncertain because of improper preservation of the specimen.

Immediately after collection, both types of hydroids readily expanded when placed in a small container of sea water. Here it was noticed that the colonies were separated by a bare strip of shell, roughly eight to twelve mm. wide, which extended from the lip of the shell across the upper part of the body whorl, passed near the apex of the shell and continued beneath the spire until it merged with the abraded area on which the shell rested. Thus a few millimetres of "no-man's land" always lay between the two colonies.

Several possible explanations of this unoccupied strip occurred to the writer but none would bear examination.

1. Environmental conditions may have differed on different parts of the shell. However, conditions must have differed more along the length than across the width of the bare strip and the two colonies were almost symmetrically arranged.

2. The bare strip may have corresponded with some structural feature of the shell. Examination of other crab-inhabited shells of *Polinices* failed to confirm this and hermit crab shells covered by *Hydractinia* alone showed no bare areas matching this one.

3. Before its occupation by the crab, the shell may have been buried to the level of the strip, being occupied by one species of hydroid in that period and by the other after its exposure. However, the shell had been exposed long enough for a limpet, *Crepidula plana,* to grow to a length of more than an inch inside its mouth.

4. Some predator, such as a snail, may have cleared this strip of its encrusting growths. It seems unlikely, though, that such an animal would eat its way across a large shell without deviating from the irregular boundary between two colonies of hydroids.

5. Both colonies may have been young and

were still growing toward each other. However, the growing edges of such colonies would scarcely be nearly parallel throughout their length.

6. It seems almost certain, then, that each colony had somehow inhibited the growth of the other when they were roughly a centimetre apart. There was no indication of the mechanism of such inhibition. However, the polyps of the two species would probably be within reach of each other's tentacles at such a distance and may simply have attacked and killed each other.

The writer must acknowledge the helpful suggestions of Edward S. Deevey, Jr., of the Osborn Zoological Laboratory, Yale University, concerning the identification of the hydroids concerned.

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SOME FACTORS AFFECTING EMERGENCE AND ESTABLISHMENT OF NATIVE GRASS SEEDLINGS IN WISCONSIN[1]

Introduction

Many attempts to re-establish native American grasses in recent years have met with only slight to moderate success. The probability that many of these indifferent results were the outcome of insufficient knowledge of seed and seedling characteristics of the native species prompted an investigation into some of the factors affecting seedling development. Studies were begun in 1949 at the University of Wisconsin and continued through 1951 with particular attention given in the winter months to the study of seedlings and seedling emergence in the greenhouse.

Dormancy and delayed germination of seed have been found to be general characteristics of native grasses. Coukos (1944) studied dormancy in 4 native grasses and found that it did not break in dry storage at room temperature until 12 months after harvest, while low temperatures and high humidity brought about a break in dormancy as early as 10 months after storage. Hoover *et al.* (1947) reported a germination at harvest of 5 to 10 per cent for *Stipa viridula* Trin. Storage of the seed for 1 to 5 years increased germination to 50 to 60 per cent. Blake (1935) concluded that native prairie seeds germinated most abundantly in the spring with a secondary peak in the fall. Stratification of grass seeds through the winter months generally resulted in higher germination. However, seedling production after thorough ripening in dry storage was found to be as high as that which followed stratification. Advantages of stratification were often lost when seeds were transferred to dry storage at relatively high temperatures.

Methods and Materials

Seedling emergence studies

Seeds of 10 species of native grasses were obtained from various Soil Conservation Nurseries during the winter of 1948–1949 as follows: *Sorghastrum nutans* (L.) Nash (Indian grass), *Andropogon gerardi* Vitman (big bluestem), *Panicum virgatum* L. (switchgrass), *Elymus canadensis* L. (Canada wild-rye), and *Elymus virginicus* L. (Virginia wild-rye) were obtained from Ames, Iowa; *Andropogon scoparius* Michx. (little bluestem), from Manhattan, Kansas; *Sporobolus cryptandrus* (Torr.) A. Gray (sand dropseed), *Eragrostis trichodes* (Nutt.) Wood (sand lovegrass), *Bouteloua curtipendula* (Michx.) Torr. (sideoats grama), *A. gerardi* and *Stipa viridula* Trin. (green needlegrass) from Waterloo, Nebraska.

A sample of seed of each species or lot was stored in a coin envelop in a dark, dry place at a room temperature of 70° F. In selecting samples from the envelopes for the studies on emergence, it was found that in florets of the species with a loosely adherent lemma and palea (*Andropogon* spp., *Sorghastrum* and *B. curtipendula*), it was necessary to separate those containing caryopses from those which were empty by checking each one with a light fingernail pressure. Both enclosed and naked caryopses were planted and no effort was made to select one or the other condition. Those species with the grain enclosed by a hard lemma and palea (*P. virgatum* and *Stipa viridula*) could not be checked in this manner, and in these instances was made on the basis of average size. *Elymus canadensis* and *E. virginicus*, which possess a closely-adherent lemma and palea, were selected on the basis of undamaged kernels. The seed of all species had been processed, where necessary, to remove awns, hairs, and glumes which would interfere with sowing with a grain drill.

Samples of 100 seeds of each species were counted out in February of 1949, 1950, and 1951

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and planted in random arrangement in each of three flats containing a mixture of one-half sand and one-half Miami silt loam topsoil. Seeds were covered to a depth of one eighth to one quarter of an inch. The flats were placed in a greenhouse with a night temperature of 60°–65° F, kept moist by watering daily with a fine sprinkler and covered with newspaper until seedlings began to emerge.

Seedling counts were made as soon as emergence began and continued until it appeared that all seedlings had emerged. Three weeks proved to be a sufficient length of time for all species except *Sporobolus cryptandrus*. Final counts were made at the end of 6 weeks. It is not certain that all viable seeds of *Sporobolus* had emerged at the end of the trial, since their emergence was extremely sporadic. Seedlings which were attacked by soil microorganisms, with resulting damping off, were marked with slivers of wood. The number of seedlings of each species which emerged from the soil in each flat was recorded as a percentage of the number of seeds sown.

Seedling growth studies

Experiments to determine the nature of growth and distribution of roots of seedlings were carried on in greenhouse studies during the winter of 1950–51. A day length of 16 hours was used, of which approximately 9 hours were natural daylight and 7 hours were artificial light. A germinated seed of each of 4 species (*Elymus canadensis, A. gerardi, B. curtipendula,* and *P. virgatum*) was planted one to a pot and grown in a greenhouse with a night temperature of 60–65° F. Three pots of each species were assigned to a position at random within a group, and the group studied each week was randomly assigned to a position on the greenhouse bench. At weekly intervals, the soil was washed from the roots of plants of the group specified for that week, and numbers and measurements of roots and leaves of the seedlings were noted. Data for *B. curtipendula* and *P. virgatum* for the eighth week was not available because of accidental destruction of the plants.

The slow growth of *A. gerardi, B. curtipendula,* and *P. virgatum* in the above study prompted repetition of the experiment in a greenhouse with a night temperature of 80–85° F. Two germinated seeds of each species were planted, one species to an 8-inch pot which had been filled with soil of the same mixture as that used in the cool greenhouse. At 7-day intervals the number and length of leaves and the number of tillers were noted. At 8 weeks, the soil was washed from the roots in each pot. The roots were counted and measured and the number of tillers or tiller and rhizome buds were noted for each plant.

Effect of weed cover on establishment of seedlings

To determine the effect of removal of weed cover on establishment of seedlings, two plots were established in the University of Wisconsin Arboretum in the spring of 1950 on an area summer-fallowed the previous year. One plot was sown to *P. virgatum* and the other to *A. gerardi.* A companion crop of oats was sown on both plots. The companion crop and volunteer weeds were mowed and removed from one-half of each plot twice during the summer of 1950. An extremely dense stand of weeds, composed of *Polygonum* spp. (smartweed), *Panicum capillare* L. (witchgrass), *Echinocloa crusgalli* (L.) Beauv. (barnyard grass), and *Chenopodium album* L. (lamb's quarters) together with the companion crop, were allowed to stand uncut on the remaining halves. Ten

TABLE I. *Time required for beginning emergence of ten species of native grasses grown in a greenhouse at a temperature of 60°–65° F. Seeds were stored dry at 70° F*

Species	Year of harvest	Days required			
		February of:			
		1949	1950	1951	Av.
Sporobolus cryptandrus	1946	9	40	14	21
Andropogon scoparius	1948	10	14	12	12
Eragrostis trichodes	1948	10	13	12	12
Andropogon gerardi (Nebraska)	1948	12	10	10	11
Andropogon gerardi (Iowa)	1948	9	10	10	10
Sorghastrum nutans	1948	10	10	11	10
Bouteloua curtipendula	1948	8	9	10	9
Panicum virgatum	1948	9	10	9	9
Stipa viridula	1947	9	9	9	9
Elymus canadensis	1948	9	7	8	8
Elymus virginicus	1948	8	7	8	8

TABLE II. *Emergence of native grass seedlings from flats kept in a greenhouse with a temperature of 60°–65° F.*

Species	Year of harvest	Average percentage of emergence			
		February of:			3-yr. mean
		1949	1950	1951	
Elymus virginicus	1948	66.0	66.3	42.7	58.3
Panicum virgatum	1948	43.3	68.7	55.7	55.9
Elymus canadensis	1948	58.3	66.0	39.7	54.7
Andropogon gerardi (Iowa)	1948	42.3	61.0	37.7	47.0
Andropogon gerardi (Nebraska)	1948	46.1	51.3	29.0	42.1
Bouteloua curtipendula	1948	71.4	32.0	7.0	36.8
Stipa viridula	1947	9.3	25.0	14.3	16.2
Eragrostis trichodes	1948	1.3	13.0	32.0	15.4
Sorghastrum nutans	1948	16.6	11.0	15.7	14.4
Andropogon scoparius	1948	19.5	4.0	4.7	9.4
Sporobolus cryptandrus	1946	22.3	1.3	2.2	8.6
Average for all species		36.0	36.3	25.5	32.6

sample quadrats, 3.3 × 3.3 ft., were counted on each of the two sections of each plot in the spring of 1951.

RESULTS AND DISCUSSION

Seedling emergence

The number of days required for beginning emergence of seedlings grown in the greenhouse at a temperature of 60°–65° F. is shown in Table I. The time required for emergence appears to be remarkably uniform for each species under conditions of relatively uniform temperature, depth of planting, type of soil, and soil moisture, if the erratic response of *Sporobolus* is discounted. Emergence of seedlings of all species was accomplished between 8 to 12 days during each of the 3 years of the study. There appeared to be no trend in the time required for emergence of seedlings with increasing age of seed.

The seed of *Sporobolus* was approximately 2½ years old when the first planting for this species was made. Its emergence at this age was quite rapid and uniform but the tests of the 2 years following showed a marked drop in emergence and a slow and prolonged emergence of those seedlings which did appear. This suggests a relatively short span of viability for this species. The shortest period required for emergence was for the two *Elymus* species, which was followed by *Stipa viridula*. The early emergence of these species at a relatively cool temperature indicated that they were better adapted to the cooler growing conditions than the other species tested. This conclusion was further borne out in the seedling growth studies of some of these species as given below. The percentage of emergence for each species is shown in Table II. The highest average emergence for the period of the trial was 58.3 per cent for *E. virginicus*, followed by 55.9 per cent for *P. virgatum* and 54.7 per cent for *E. canadensis*. The lowest average was 8.6 per cent for *Sporobolus cryptandrus*, followed by 9.4 per cent for *A. scoparius*. Compared to emergence of seed 6 months old, *A. scoparius*, *Sorghastrum nutans*, *B. curtipendula* and *Sporobolus cryptandrus* showed a decrease in emergence when seed that was approximately 18 months old was planted, with a slight increase when seed that was approximately 30 months old was used, except for *B. curtipendula*. Of the 10 species tested, only *Eragrostis trichodes* continued to increase in percentage of emergence as the seed used increased in age. The remaining species showed a tendency to increase in percentage of emergence when seed that was 18 months old was planted instead of that which was 6 months old. In *Stipa viridula*, the peak in emergence occurred when seed 30 months old was planted, although in this instance emergence of seed 6 months old was not known.

Seedling growth

The most striking feature of the experiment in the cool greenhouse was the rapid growth of roots and tops of *Elymus candensis* as compared to *A. gerardi*, *B. curtipendula*, and *P. virgatum*. *E. canadensis* was observed to have 4 seminal roots, while *A. gerardi*, *P. virgatum*, and *B. curtipendula* had only one active seminal root. The average total length of seminal and adventitious roots (Table III) of *E. canadensis* (1,356 mm.) was about 12 times that of *A. gerardi* (114 mm.). The average total length of leaves of *E. canadensis* at 8 weeks (1,342 mm.) was 7 times that of *A. gerardi* (186 mm.). At 7

weeks, the average length of roots of *E. canadensis* was 1,033 mm., which was more than 11 times that of *B. curtipendula* and 9 times that of *P. virgatum.*

The average total length of leaves per plant for *E. canadensis* at 7 weeks (954 mm.) was more than 15 times that of *B. curtipendula* (62 mm.) and more than 8 times that of *P. virgatum* (115 mm.).

P. virgatum, and *A. gerardi* had growth characteristics which were alike, while *B. curtipendula* was slowest in development over the 7-weeks' period. The latter species, however, being inherently of smaller stature and with shallower roots, was not expected to show the quantitative development of the lowland species. The upland characteristic of drought resistance was strongly suggested in the rapid initial development of the seminal root of *B. curtipendula* and the more extensive development of roots as compared with leaves at 7 weeks. Where there was a tendency for the combined length of leaves to approach or equal the length of first-order roots in the other 3 species at 7 and 8 weeks, this was not readily apparent in *B. curtipendula* under the conditions of growth in the greenhouse.

The total number of roots of *E. canadensis* at 7 and 8 weeks was 11, as compared with 2 each for *A. gerardi, P. virgatum,* and *B. curtipendula.* At 8 weeks, *E. canadensis* had 6 leaves as compared with 4 for *A. gerardi,* and at 7 weeks, it had 5 as compared with 2 each for *P. virgatum* and *B. curtipendula.*

Responses of *A. gerardi, P. virgatum* and *B. curtipendula* to the higher temperature of the warm greenhouse were much greater than for *E. canadensis.* For *A. gerardi,* the average number of roots increased 3 times (from 2 to 6), while the total length of roots increased nearly 12 times (from 114 mm. to 1,350 mm.), and the total length of leaves increased nearly 10 times (from 186 mm. to 1,789 mm.). The number of leaves of *P. virgatum* increased from 2 to 5, and the total length of leaves from 115 mm. to 894 mm. at 7 weeks; in *B. curtipendula* the number of leaves increased from 2 to 5 and the total length of leaves from 62 mm. to 908 mm. at 7 weeks.

In *E. canadensis,* on the other hand, the number of roots increased only a fraction more than twice (from 11 to 26), as compared to the cool greenhouse, and the average total length of roots increased from 1,356 mm. to 4,812 mm.

TABLE III. *Comparative data on root and top characteristics of four species of native grasses grown in pots in greenhouses having two different temperatures*

Species	Age in weeks	Roots		Leaves	
		Av. no.	Av. total length, mm.	Av. no.	Av. total length, mm.
Temperature of 60°–65° F					
Andropogon gerardi	7	2	—	4	122
	8	2	114	4	186
Bouteloua curtipendula	7	2	90	2	62
	8	—	—	—	—
Elymus canadensis	7	11	1,033	5	954
	8	11	1,356	6	1,342
Panicum virgatum	7	2	116	2	115
	8	—	—	—	—
Temperature of 80°–85° F					
Andropogon gerardi	7	—	—	7	1,222
	8	6	1,350	9	1,789
Bouteloua curtipendula	7	—	—	5	908
	8	8	1,243	6	1,249
Elymus canadensis	7	—	—	18	3,244
	8	26	4,812	20	3,755
Panicum virgatum	7	—	—	5	894
	8	6	1,147	6	1,158

The number of leaves increased from 6 to 20, and the average total length of leaves from 1,342 mm. to 3,755 mm. The first tiller appeared at 4 weeks, and there were 3 tillers at 8 weeks. In the cool greenhouse, no tillers had emerged from the leaf sheath at 8 weeks.

Inspection of the seedling after removal of soil from the roots revealed two rhizome buds in *E. canadensis,* two rhizome buds and a number of tiller buds in *P. virgatum,* two tiller buds in *B. curtipendula,* two rhizome buds and a number of tiller buds in *A. gerardi.*

First-order roots of *B. curtipendula* were extremely fine; the youngest roots of *E. canadensis* were much finer than the older. All roots of *P. virgatum* were coarse, while in *A. gerardi* the single seminal root, 225 mm. long, was extremely fine and profusely branched with lateral extensions up to 125 mm. long. Adventitious roots of *A. gerardi* had the greatest diameter of any of the species grown and they were much less finely branched than the seminal root.

The appearance of the root systems as they developed in the warm greenhouse are shown in the photograph in Figure 1.

FIG. 1. From left to right: seedlings of *Elymus canadensis, Bouteloua curtipendula, Andropogon gerardi,* and *Panicum virgatum* grown in a greenhouse with a night temperature of 80°–85° F and photographed when eight weeks old. Lines are one inch apart.

Effect of weed competition on seedlings

Counts were made on the competition plots in the spring of 1951, using a 3.3 × 3.3-foot quadrat. The data from the portions of the plots from which the weeds and companion crop were removed and those from the area on which the weeds and companion crops were not removed are presented in the tabulation below as the sum of the 10 samples from each area.

A. gerardi		*P. virgatum*	
Clipped	Not clipped	Clipped	Not clipped
119	15	441	128

SUMMARY

Experiments were conducted in the greenhouse over a period of 3 winter seasons to determine the percentage of emergence of 10 species of native grasses. Investigations also included measurements of roots and tops of *E. canadensis, A. gerardi, P. virgatum,* and *B. curtipendula* seedlings grown at temperatures of 60°–65° F and 80°–85° F.

The peak of germination under greenhouse conditions was higher the first year after harvest than in the following years for *A. scoparius* and *B. curtipendula.* Seeds of *A. gerardi, E. canadensis, E. virginicus,* and *P. virgatum* produced the most seedlings when planted the second year after harvest. Those of *Stipa viridula* and *Eragrostis trichodes* produced the most seedlings when planted the third year after harvest. Seeds of *Sorghastrum nutans* grew equally well when planted the first, second, or third year after harvest. The average number of seedlings of all species which emerged under conditions of greenhouse culture was less than 50 per cent of the sound seeds planted.

The average total length of leaves per plant of *E. canadensis, A. gerardi,* and *P. virgatum* was slightly less than the average total length of first-order roots per plant during the period of the experiment. With *B. curtipendula* the leaf development was much less extensive than the root growth during the same period.

E. canadensis produced an average of 4 seminal roots. *A. gerardi, P. virgatum,* and *B. curtipendula* had only one active seminal root.

E. canadensis grew rapidly, and *A. gerardi, P. virgatum,* and *B. curtipendula* grew very slowly at a greenhouse temperature of 60°–65° F. The last 3 species grew more rapidly at 80°–85° F than at 60°–65° F, and the percentage of increase in their rate of growth was greater than for *E. canadensis* at the higher temperature. However, even at the higher temperature, the total length of first-order roots and total length of leaves of *E. canadensis* was still more than twice that of any of the other species at 8 weeks of age, and it produced 3 times at many roots and twice as many leaves as any of the other species investigated.

Experimental plots established on land sum-

mer-fallowed for one season revealed that competition from weeds and a companion crop during the year of seeding reduced the density of pure seedings of *P. virgatum* and *A. gerardi* to approximately one third and one eighth, respectively, of that on the clipped portions of the plots.

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A FIELD STUDY OF PEROMYSCUS POPULATIONS IN GULF HAMMOCK, FLORIDA

Introduction

In another paper recently accepted for publication (Pearson *in press*), some of the general ecological characteristics of the Gulf Hammock region in Levy County, Florida, are presented in conjunction with an account of the mammals of that region. An integral part of this general survey was concerned with a study of Peromyscus populations, and this study is discussed here. Of interest in the study were (1) the relative abundance of the two species of Peromyscus, (2) the possible factors influencing population size, and (3) some of the effects of different degrees of population crowding. Trapping efforts were intensified in one plot of approximately nine acres in the hardwood forest, a map of which is shown in Figure 1, during the period from September 1949, to September 1950. This plot was thought to be typical because it included closely interwoven forests of mesic hammock (a climax forest, dominated by broadleaved evergreen trees, that is flooded only under the most extreme conditions), hydric hammock (an area dominated by broadleaved evergreen trees and occasionally flooded for short periods), and swamp (an area dominated by deciduous trees that is flooded for the majority of the year).

Plant Communities

The most intense trapping operations in this plot centered on the mesic ridge community that parallels Otter Creek. In this mesic hammock, water oak (*Quercus nigra*),[1] pignut hickory (*Carya glabra megacarpa*), sweetgum (*Liquidambar styraciflua*), and cabbage palm (*Sabal palmetto*) were most abundant. Of less abundance in the arboreal vegetation were magnolia (*Magnolia grandiflora*), cow oak (*Quercus prinus*), laurel oak (*Quercus laurifolia*), live oak (*Quercus virginiana*), loblolly pine (*Pinus taeda*), and ironwood (*Carpinus caroliniana*). Generally, shrubs covered this mesic ridge in a dense layer three to six feet in height, but there were several small areas of sparse shrub growth. Saw palmetto (*Serenoa repens*) and yaupon (*Ilex vomitoria*) were most abundant, while shrubs of less importance were sparkleberry (*Vaccinium arboreum*), blackhaw (*Viburnum corymbosum*), French mulberry (*Callicarpa americana*), staggerbush (*Xolisma fruticosa*), gallberry (*Ilex glabra*), and arrowwood (*Viburnum semitomentosum*). A panic grass (*Panicum joori*) was recorded in the exceptionally sparse herbaceous vegetation.

The hydrophytic communities, occurring between the mesic ridge and the creek in the plot, were formed by hydric hammock, swamp and intergrades thereof. The hydric hammock was dominated by water hickory (*Carya aquatica*), laurel oak, and cabbage palm, with ironwood forming a dense canopy of small trees. Other trees in this canopy were sweetgum, loblolly pine, and ash (*Fraxinus* sp.). Shrubs and small trees in this layer were tough dogwood (*Cornus stricta*), parsley hawthorn (*Crataegus marshallii*) and blackhaw. A dense herbaceous layer included *Panicum* spp., *Paspalum* spp., partridge berry (*Mitchella repens*), poison ivy seedings (*Toxicodendron radicans*), wood grass (*Oplismenus setarius*), mist flower (*Conoclinium coelestinum*), *Centella repanda, Pluchea* sp., and *Tubiflora* sp.

In the swamp that covered a very small part of the plot, prominent trees were red maple (*Acer rubrum*), water locust (*Gleditsia aquatica*), black gum (*Nyssa sylvatica biflora*), bald cypress (*Taxodium distichum*), and laurel oak. Shrubs were Virginia willow (*Itea virginica*), parsley hawthorn, blackhaw, and buttonbush (*Cephalanthus occidentalis*). Herbs found here were mist flower, smartweed (*Persicaria* sp.) lizard's tail (*Saururus cernuus*), blue flags (*Iris* sp.), and *Justicia* sp.

[1] Nomenclature for trees according to West and Arnold (1946); other plant nnames according to Small (1933).

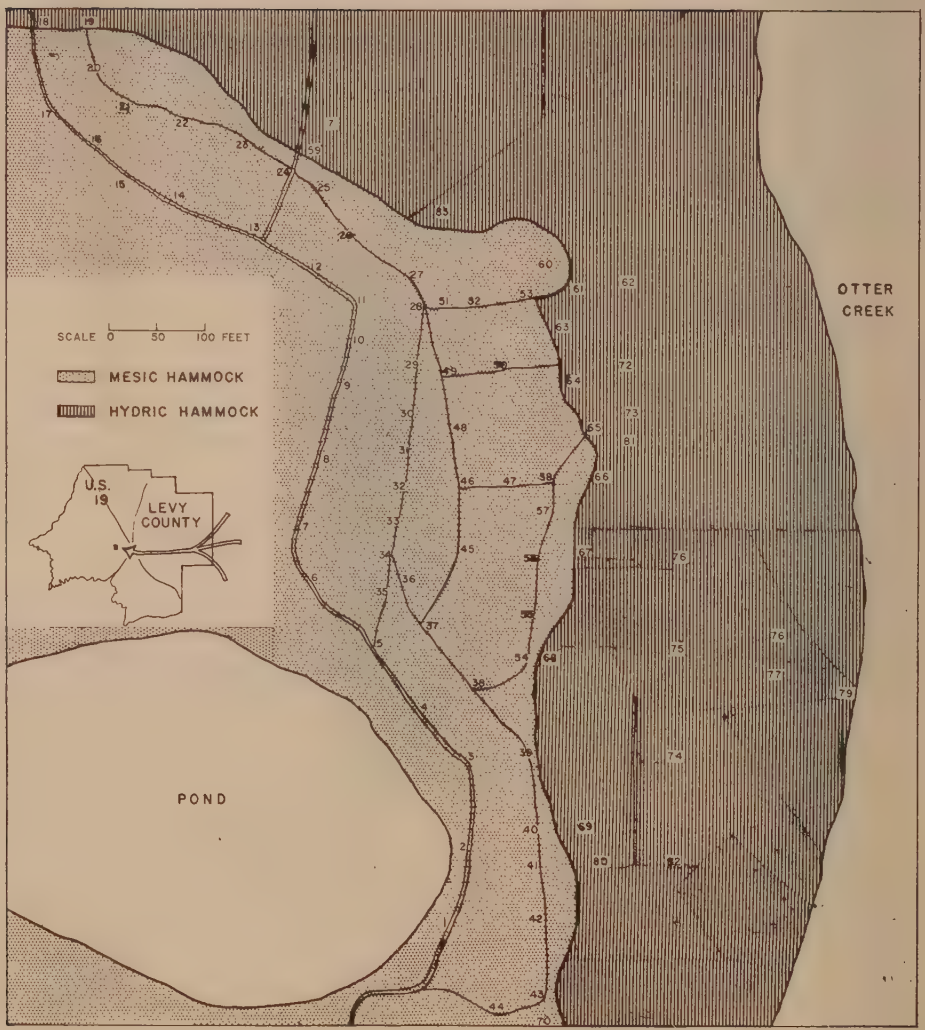

FIG. 1. A study plot located, as shown on insert, in Levy County, Florida. Trapping stations are indicated by numbers 1–83.

GENERAL ECOLOGICAL CONSIDERATIONS

Cover and nest sites for Peromyscus were very abundant in this plot. In the mesic portion there were numerous windfalls, hollow bases of living trees, rotting stumps and other debris left by the lumberman. In the hydrophytic communities of the plot there were even more available cover and nest sites than in mesic hammock, as there were many rotten logs and much other debris deposited by flood waters of the creek.

It is thought that a major factor influencing the Peromyscus populations here was the food supply afforded by the acorn mast. In their study of the factors influencing deer and turkey and the squirrel populations of the area Swindel (1949) and Jennings (1951) studied the productivity of the oak species. The studies were made during the years 1948, 1949, and 1950, and Jennings concluded that the acorn production in 1948 was exceptionally high, whereas mast production in 1949 was almost non-existent. The few acorns that were produced had been utilized by the middle of October 1949. The

production of 1950 was somewhat better than in 1949, but even this year was classed as a poor acorn year.

In this plot several species of animals competed with Peromyscus for the available food supply. This population density of gray squirrels (*Sciurus c. carolinensis*) was relatively high in the fall and winter of 1949 (Jennings 1951), and they probably competed for some foods. Fourteen wood rats (*Neotoma f. floridana*) were trapped 37 times in the plot, whereas cotton rats (*Sigmodon h. hispidus*) were recorded only sporadically in the plot (four individuals trapped five times). There were far more cotton rat traps available than there were traps for wood rats. The opossum (*Didelphis virginiana pigra*) was trapped only once by the author and on a few occasions by Jennings (personal communication). Probably of most importance in the competition for the oak mast were the semi-wild range hogs that were so very abundant in the area.

Among the possible predators of *Peromyscus* in the 1949–50 season, wildcats (*Lynx rufus floridanus*) were abundant in this area and their tracks were regularly observed in the plot. Barred owls (*Strix varia*) were seen often enough in the immediate vicinity of the plot to be ranked as abundant. Although no records of the rat snake (*Elaphe obsoleta williamsi*) and the indigo snake (*Drymarchon corais couperi*) were obtained for the plot they were relatively abundant in similar adjacent habitats.

Another ecological factor to be considered is the fluctuation of water level. Rainfall is unevenly distributed throughout the year with June, July, August, and September being the months of heaviest rainfall, while the months of least precipitation are November, April, and May (Mitchell and Ensign 1928). During the rainy seasons most, if not all, of the hydrophytic communities were submerged when the channel of Otter Creek was unable to handle the surface runoff. During the dry periods the inter-stream areas are thoroughly drained, and Otter Creek occasionally becomes sluggish and stagnant. In this study, the hydrophytic communities were entirely flooded during September and October 1949, and July 1950, and they were partially inundated during November 1949, and March and August 1950. The hurricane of September 5, 1950, brought rains which flooded the entire plot for several days. On the other hand, during December 1949, January, February, April, May, and June 1950, the hydrophytic communities of this plot were almost or entirely dry.

Methods

In studying the Peromyscus populations the majority of the trapping effort was expended in the mesic hammock, and during the various trapping periods listed in Table I hydrophytic communities were only trapped intensively when the water table was low. Trapping was done with the Sherman live trap that measures $2 \times 2\frac{1}{2} \times 6\frac{1}{2}$ inches. Traps were spaced from

Table I. *A summary of trapping results in a nine acre forest plot in Gulf Hammock, Florida*

Last night of trapping period	Number of nights trapped	Trap nights		*P. gossypinus*		*P. nuttalli*	
		Mesic community	Hydric community	Total catch	% retakes	Total catch	% retakes
9–24–49	2	120	—	30	17	—	—
10–1 –49	2	92	—	43	56	—	—
10–9 –49	3	57	18	34	76	—	—
10–30–49	2	100	20	41	80	1	—
12–4 –49	2	110	10	35	77	2	50
12–17–49	1	55	5	11	73	4	25
1– 7–50	1	15	15	6	83	2	50
1–21–50	2	46	38	15	67	10	60
2–26–50	2	44	40	12	92	5	80
3–12–50	1	40	20	8	100	4	100
4–2 –50	2	74	10	5	80	6	80
4–16–50	2	62	22	7	100	6	80
5–8 –50	2	72	28	7	100	11	72
6–16–50	3	99	51	16	88	9	89
7–2 –50	3	120	30	13	100	10	100
7–16–50	3	135	15	6	100	9	89
8–3 –50	3	129	21	8	88	7	100
8–16–50	3	111	39	18	72	2	100
8–30–50	4	134	64	21	90	3	100
9–22–50	1	31	—	2	100	—	—
Totals	44	1,646	446	338		91	

25 to 100 feet apart, usually at 50 feet. No effort was made to locate traps exactly in a grid system, but rather they were placed in sites, indicated by numbered stations on Figure 1, thought to be most suitable for mouse capture. Traps were usually placed on the ground surface inside hollow logs, in rotten stumps, on floating logs, on high stumps, and in underground burrows. Oatmeal and white and yellow cornmeal were used as baits for these traps.

Sixty-eight of the 89 cotton mice (*Peromyscus gossypinus gossypinus*) and 15 of the 18 golden mice (*Peromyscus nuttalli aureolus*) that were trapped in this plot were examined, marked by a system of ear clippings and punches as described by Burt (1940), and released at their point of capture. The 68 marked cotton mice were retaken 249 times; the maximum number of recaptures per individual was 21. The 15 marked golden mice were retaken 73 times; the maximum number of recaptures per individual *nuttalli* was 19. The animals that were to be marked were emptied from the trap into a cotton sack, from which they were easily recovered for examination.

Fluctuations of Population Size

The abundance of Peromyscus for this plot is given in Figure 2. This population estimate is based upon the known number of individuals taken during a trapping period, plus individuals trapped on *both* earlier and later dates. For example, if an individual was taken in the first trapping period, but was not taken again until the fourth trapping period it would be counted as a member of the population for the first, second, third and fourth periods. The assumption is made that even though an animal might not be trapped during a period its capture at both earlier and later periods indicates a possible failure of trapping methods and not necessarily a movement of its range out of and back into the plot. It can be seen from Figure 2 that from late September through early December 1949 the cotton mice were apparently at peak abundance; during that time only three golden mice were taken. With the decrease in cotton mouse abundance in mid-December, the golden mice seemed to assume a more important position in the mesic community, although they

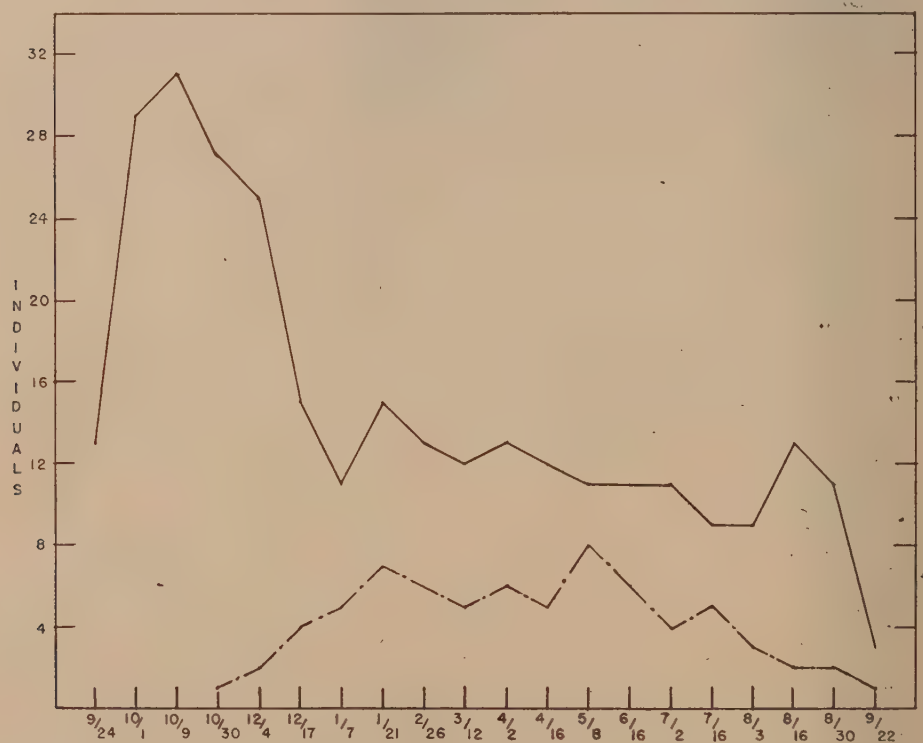

Fig. 2. Numbers of Peromyscus caught during 1949–50 on a nine-acre study plot in north Florida. Solid line represents the cotton mouse, *P. gossypinus*, and the broken line refers to the golden mouse, *P. nuttalli*.

TABLE II. *Number of trap nights necessary to catch one individual of the two species of* Peromyscus *during each of the trapping periods. The plus sign indicates that no individuals were trapped with the number of trap nights listed*

Date	*gossypinus*	*nuttalli*	Date	*gossypinus*	*nuttalli*
9–24	4	120+	4–2	16.8	12.3
10–1	2.1	92+	4–16	12.0	10.3
10–9	2.2	57+*	5–8	14.3	6.5
10–30	2.9	100.0	6–16	9.4	11.0
12–4	3.4	55.0	7–2	11.5	12.0
12–17	5.5	13.7	7–16	25.0	15.0
1–7	5	7.5	8–3	18.8	18.4
1–21	5.6	4.6	8–16	8.3	55.5
2–26	7	8.8	8–30	9.4	44.7
3–12	7.5	10.0	9–22	15.5	31.+

* In the calculation of trap difficulty for *P. nuttalli* only trap nights in mesic hammock are used since these mice were never trapped in hydric hammock.

never were more abundant than the cotton mice. The golden mice were never trapped in the hydrophytic communities.

It is thought that the trapping results represent fairly accurately the populations of Peromyscus in the plot since on only two occasions were there less than 75 per cent *gossypinus* retakes after mid-October 1949, and all animals trapped were retakes in six periods for *gossypinus* and during five periods for *nuttalli*. The number of retakes refers to the number of animals that had been marked in previous trapping periods.

A reciprocal relationship between these species is also shown by data in Table II on the degree of trapping difficulty. If the total number of trap nights for each trapping period is divided by the respective catch for that period, the result is the number of trap nights necessary to catch one individual, thus giving a measure of the degree of trapping difficulty. The *nuttalli* were captured only a few times during the peak *gossypinus* abundance, but were taken with greater ease when the *gossypinus* population was decreased.

To what can the rise of *nuttalli* captures be ascribed? Four hypotheses are: (1) that there was an increase in the absolute number of golden mice in the area with the decrease in cotton mouse abundance, (2) that the probability of capture was greatly increased by the lowered abundance of cotton mice, and that the absolute number of *nutttalli* remained nearly the same throughout, (3) that with the decrease of cotton mice, the golden mice moved from another habitat, or (4) the golden mice moved from the arboreal to the epigeic strata of the community and were more trappable. No evidence is available concerning the first hypothesis. It may be noted relative to hypothesis (2) that on no occasion were more than half of the available traps filled with *gossypinus*. Little is known of a movement of *nuttalli* from other habitats, but one golden mouse was trapped by A. J. Rogers in January 1952, a year and a half after its release, within 100 feet of its release point. This may indicate that there was no general movement since 1950. Relative to hypothesis (4) it is noted by Pearson (in press) that on eight occasions these mice entered burrows on or near the ground, which is contrary to their usual behavior as reported by Ivey (1951). Despite continued search, only two arboreal nests were found. Dalquest (1941) found that in a marshy habitat in Washington if he removed Peromyscus he was better able to trap certain insectivores, an interaction seemingly similar to my hypothesis (2). He reports that *Sorex vagrans* was confined to the marshy habitat while *Sorex trowbridgi* was most common in dry fir woods. When *vagrans* was abundant in the marsh *trowbridgii* was absent, or nearly so, but when the *vagrans* population was low, *trowbridgii* became quite common in the marshy habitat. As called for by my third hypothesis, we see here a response to a decrease in interspecific population pressure. Further research is necessary to determine whether the golden mouse will change its occupancy of community strata in response to population pressure changes.

Was this apparent reduction in the *gossypinus* population size restricted to this plot or did it occur generally over the area? Trapping was carried on in five other plots previous to and after this crucial period where the trapping methods were the same and where the trapping was done under similar weather conditions. A comparison of the number of trap nights necessary to catch one cotton mouse in these five plots is as follows: *a*, July 9, 1949, and June 22, 1950, 10.5 and 13 trap nights; *b*, June 25, 1949, and June 22–24, 1950, 4.3 and 120-plus trap nights; *c*, November 12, 1949, and August 5–6, 1950, 2.7 and 11.4 trap nights; *d*, June 18, 1949, and June 27–29, 1950, 4.5 and 30 trap nights; *e*, June 18, 1949, and June 27–29, 1950, 3 and 45 trap nights. Since in these five plots the difficulty of trapping was increased after the winter of 1949–50, it is concluded that there was a general population decrease throughout the area.

The cause for this population decrease is not known. However, there seems to be a good correlation between the exceptionally good acorn production of 1948 and the high cotton mouse population level, and contrariwise between the failure of the 1949–50 mast production and the strong reduction of the mouse population.

Another and possibly more important factor contributing to the decline of these populations during this winter period might be a low rate of reproductive success. During the fall of 1949, a number of females were judged to be lactating. Yet only one juvenile or young adult individual was recorded in this plot from January to September 1950. This female appeared June 14, 1950, with a juvenile pelege and it was recorded in the plot until August 30, 1950. The winter period should ordinarily be the time of peak reproduction of cotton mice and a peak occurrence of young individuals should follow (Pournelle 1952). It is possible that the lowered reproductive success during times of excessive population density is of major importance here. A sizable literature on reduction of population size is available and this is well summarized by Allee *et al.* (1949). It should be noted that in this field situation a good correlation exists between extreme reduction of a food item as well as an almost total absence of production of young, and a sudden reduction of *gossypinus* numbers in December 1950.

Longevity

These Peromyscus data are not suitable for construction of a life table, but suggestions of their longevity under natural conditions may be obtained. It is seen that of the 68 cotton mice marked in this study 22 were taken during one trapping period only and hence were probably either transients or taken too late in the study for possible recapture. Of the remaining 46 individuals, 13 were retaken more than 100 days after first capture. These 13 individuals were handled and known to be alive for periods of 107, 126, 149, 163, 201, 207, 215, 229, 270, 292, 337, and 357 days. One animal trapped in each of the three periods in August 1950 was captured by Mr. A. J. Rogers (personal communication) on May 17, 1952, indicating a life span of nearly two years.

Likewise, of 15 *nuttalli* marked in the study area five were taken only during one trapping period. Six of the remaining ten individuals are known to have lived more than 90 days. Five of these six individuals were taken over periods of 93, 107, 114, 233, and 235 days. The sixth individual was a male last taken by the author on August 30, 1950, but Mr. Rogers trapped this animal in its same range on January 26, 1952. That makes its longevity at least 2 years and 27 days, and since it was an adult on first capture it was at least two and a half years old.

Factors Affecting Movements

Concerning the range of individual Peromyscus, it is interesting to compare in Table III the distance between the point of release and recapture under crowded (through December 4, 1949) and under non-crowded (after mid-December 1949) conditions. It will be noted that under the former, two-thirds of the *gossypinus* captures were made less than 125 feet from the points of release, while under less crowded conditions less than half (47 per cent) of the captures were made at less than 125 feet. Testing the frequency distribution in categories of less than and more than 125 feet under crowded and non-crowded conditions by Chi-square, we obtain a value of 9.54 with one degree of freedom. Since the probability that this is a random distribution is less than one per cent, the difference between the number of mice moving less than 125 feet under crowded and non-crowded conditions is statistically highly significant. The average distance between release point and capture site under crowded conditions was 103 feet, while under less crowded conditions the average distance was 142 feet. It is possible that a similar mechanism is in-

Table III. *A comparison of the number of individuals trapped at various distances between release and recapture sites*

Feet	*Peromyscus gossypinus*				*Peromyscus nuttalli*
	Through 12–4–49	After 12–4–49	Males	Females	After 12–4–49
0– 25	31 (28%)	33 (24%)	40 (25%)	24 (27%)	12 (17%)
25– 75	22 (20%)	11 (8%)	20 (12%)	13 (15%)	17 (24%)
75–125	22 (20%)	21 (15%)	23 (14%)	20 (23%)	15 (21%)
125–175	14 (12%)	23 (17%)	27 (17%)	10 (12%)	18 (26%)
175–225	12 (11%)	16 (12%)	21 (13%)	7 (8%)	5 (7%)
225–275	3 (2%)	14 (10%)	14 (9%)	3 (3%)	— —
275–325	— —	8 (6%)	5 (3%)	3 (3%)	1 (1%)
325–375	5 (4%)	5 (4%)	6 (4%)	4 (5%)	2 (3%)
375–425	2 (2%)	4 (3%)	4 (2%)	2 (2%)	1 (1%)
425–475	1 (1%)	2 (1%)	1 (1%)	2 (2%)	— —
Totals	112	137	161	88	71

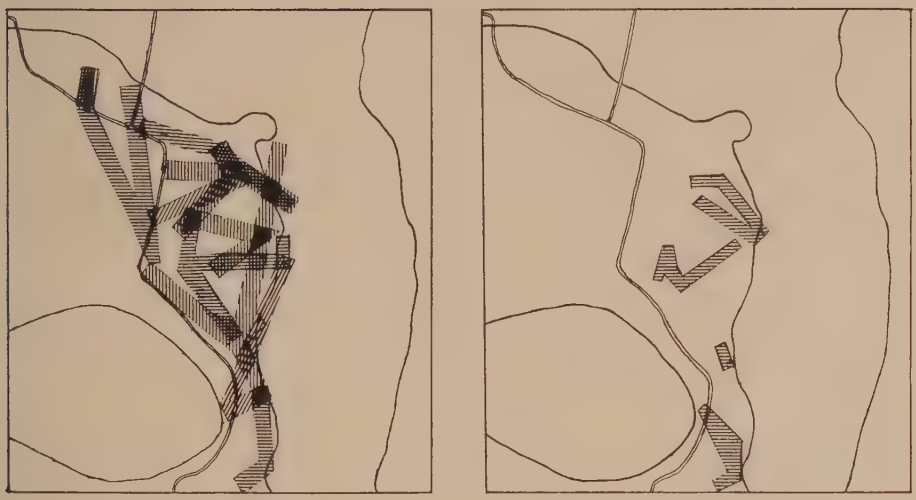

FIG. 3. Represented on these maps of the study plot are ranges where individual *P. gossypinus* were trapped. Note how the ranges of the males overlap, while those of females do not.

volved here, as in the decrease of territorial range under crowded as compared with uncrowded colonies of fiddler crabs (Crane 1941).

Likewise, it is seen from Table III that for *gossypinus* there is a difference between males and females for the distance between release point and recapture site. A larger percentage of females (63 per cent) was taken within 125 feet of their release point than were the males (51 per cent). The Chi-square value obtained from the test of these frequencies is 3.96 with one degree of freedom. The probability that this approaches a random distribution is slightly less than five per cent. This indicates a statistically significant difference between the movements of males and females. There was an average release-recapture site distance of 129 feet for the males as compared with a smaller mean of 112 feet for the females.

From a study of the points of capture of *gossypinus* in the plot comes the conclusion that, in general, the trap-ranges (areas where individuals were trapped) of individual males overlap, while the trap-ranges of females do not. Representation of all captures would prove too lengthy and is probably not practical. Therefore, only the period from September 23, to October 30, 1949, is figured, and for this period all the trap-ranges of individuals trapped more than four times are given in Figure 3. It is seen the trap-ranges of males do overlap considerably while those of the females are generally more consolidated and do not overlap. It is possible that the greater degree of overlap of male ranges is correlated with the greater abundance of individuals of this sex.

An examination of capture sites also suggests that *gossypinus* may change its range relative to water level fluctuation. As would be expected, the mice are largely confined to the higher mesic hammock during high water (Fig. 3), and expoit the hydrophytic communities when they are not flooded. Exemplifying this response to water level fluctuation are the movements of a male no. 55 and a female no. 143. The male was trapped on or at the edge of the mesic ridge (at stations 6, 37, 38, 40, 54, 61, as shown in Fig. 1) during high water stages in September, October, and during a drier period in December 1949. This male was taken during months of low water level in February, April, May and June 1950, mostly in the hydric community (stations 3, 67, 75, 74, 76, and 79), but with the appearance of the rainy season he was again trapped on the mesic ridge (station 54). The female was trapped in mesic habitat in December and on January 7, 1950, and during wet weather in March 1950 (stations 25, 50, 52), but meanwhile was observed in hydric situations on January 20 and during February 1950 (stations 65, 72). In June 1950 this female was trapped in both mesic and hydric communities (stations 53, 67, 67, 77), while in July and August she was mostly trapped on the mesic ridge (stations 51, 26, 73).

Significant changes in the trap-ranges of resident males were apparently correlated with the death of a resident male no. 104, on July 1,

1950, and with the appearance of high water conditions from late June through August 1950. After the death of no. 104, which had occupied a northern portion of the plot (stations 24, 27, 31, 37, 50, 53, 68, 72), male no. 133 moved its range about 200 feet northward (from stations 2, 5, 40, 68 to stations 34, 37, 45, 47, 54, 75, 76). Male no. 70 had been recorded in the hydric communities (stations 67 and 79) in dry periods between March and June 16, 1950, and on the mesic ridge (stations 2, 42, 44, 69, 74), but with the death of no. 104 and higher water level no. 70 moved back onto the mesic ridge and northward (stations 4, 40, 2, 1). Male no. 173 was first captured in this plot on August 3, 1950, and subsequent captures indicate that it apparently filled the northern portion of the old range of no. 104 (stations 26, 27, 31, 72, 75, 76). Thus it appears that we have here a change in range correlated with water level fluctuation, and a response by at least three males to a vacuum left by the removal of another male resident.

Concerning the ranges of *nuttalli*, with the exception of a male trapped in the south part of this mesic ridge (stations 1, 3, 34) and one female located in the northern part of the plot (stations 13, 15, 21, 24, 25, 45), all the resident males and females were clustered in a restricted area of about one acre of dense shrubby habitat on the mesic ridge (area circumscribed by stations 9, 10, 12, 50, 47, 46, 32).

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Summary and Conclusions

1. Estimates of population size indicate that *Peromyscus gossypinus* was abundent in the fall of 1949, but suffered a decrease in December 1949. This decrease was of a general nature throughout the Gulf Hammock area.

2. With a decrease in *gossypinus* in the study plot there was an increase in the number of *Peromyscus nuttalli* trapped. A reciprocal relationship between the occupancy of the given habitat by the two species is inferred from a study of the number of captures and from the relative degrees of trapping difficulty for the species throughout the year.

3. A good correlation was shown between the success of acorn production for the years 1948, 1949, 1950, and the level of *gossypinus* populations. It is postulated that a reduced reproductive potential was important to changes in the *gossypinus* density, and possibly it provided the mechanism whereby the changes were brought about.

4. Records of longevity of these species suggested that at least 28 per cent of the resident population of *gossypinus* lived at least 100 days after reaching adulthood, with one individual living nearly two years under natural conditions. Sixty per cent of the resident *nuttalli* population lived longer than three months after reaching adulthood and one individual survived nearly two and a half years.

5. An analysis of the ranges over which Peromyscus were trapped is given. Generally, the trap-ranges of male *gossypinus* overlapped, while those of females did not. There is a possible correlation between the higher degree of overlap in the males and greater number of males than females present. The ranges of cotton mice were dynamic in that they fluctuated with changes in water level and in response to a removal of a resident individual. Capture records indicate that the majority of resident *nuttalli* were concentrated in a small area of shrubby mesic hammock.

6. Statistically, a highly significant difference was observed between the number of cotton mice moving less than 125 feet between release and recapture sites under crowded as compared with non-crowded population conditions. This indicates that smaller movements between release and recapture sites are correlated with crowded conditions.

7. There was a significantly greater number of females moving less than 125 feet between release and recapture sites than males, whereas there was a greater frequency of males moving more than 125 feet than of females. This apparently indicates that males tend to move further and females a shorter distance between release and recapture sites.

8. A general description of ecological factors in a Peromyscus habitat of north Florida is presented.

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NEAR EXTINCTION OF THE CELTIS PETIOLE GALL INSECT IN NORTH GEORGIA

While engaged in a research project involving the insect *Pachypsylla venusta,* the writer observed an almost complete annihilation of the species in a large area of north Georgia in one night.

Pachypsylla venusta, Osten Sacken, is a small, green, hump-backed psyllid whose nymphs induce a petiole gall on the leaves of *Celtis* (hackberry) trees. The nymphs overwinter in the dead galls which are very persistent, remaining attached for several years on the twigs. With the onset of mild weather in the spring, the nymphs undergo their last moult; the adults emerge from the galls and deposit eggs on the inner surfaces of the unfolding bud scales of *Celtis* trees. Upon hatching, the young nymphs crawl up the developing stem to leaves near its tip and feed on the petioles and leaf bases. The stimulus produced by the feeding nymphs induces proliferation of the tissues adjacent to those being fed upon, resulting in the development of a polythalamous (several chambers each with an insect) gall. Only one generation of young is produced each season.

When the writer first began field work in Georgia in the spring of 1948, he was impressed with the large number of these petiole galls on the leaves of *Celtis.* Practically all *Celtis* trees growing in places exposed to the wind were heavily infected. The insects inducing the galls were obviously wind-borne, for trees in sheltered ravines and in dense woods showed no infection except for those branches which extended above or beyond the wind break. This condition had apparently prevailed over a period of many years, for large numbers of dead galls could be found clinging to branches. No doubt the heavy infection had been casually observed by local dendrologists for a long time because they gave the petiole galls as a distinguishing characteristic of *Celtis* in this area.

During the first two weeks of April, 1949, there occurred a period of mild weather which brought about the swelling of buds and development of the young branches. The warm weather also resulted in the emergence of the adult *Pachypsyllids* from the galls, deposition and hatching of their eggs, and the onset of gall formation. On the night of April 16, 1949, a heavy frost killed most of the young vegetation in north Georgia. Later, new growth occurred, but trees which had borne hundreds of galls in preceding years now produced none or very few. In the spring of 1950, the writer was engaged in a research project on these galls and was unable to collect more than a hundred within a fifty-mile radius of Athens. The 1951 and 1952 seasons showed no improvement over 1950. Only infected trees which had been partially sheltered during the frost bore evidence of infection. The frost occurred just as the young nymphs were beginning to feed; hence, the population was destroyed because of the destruction of the food supply. Since the adults of *Pachypsylla venusta* emerge from the galls with first onset of warm weather and are short-lived, it is obvious that a second population in a season could not occur. Inasmuch as the insects are wind-borne, the trees in the exposed places were most heavily infected and most severely damaged by the frost. Sheltered trees whose foliage survived the frost were less likely to be infected, or if infected, not exposed to the wind to provide further distribution of the insects.

Summary

The complete dependence of the insect *Pachypsylla venusta* upon *Celtis* leaves for food and the production of but a single generation of young each year have resulted in a near annihilation of this species in a single night by a killing frost in north Georgia.

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NOTES ON COPEPOD ENCYSTMENT

The major contributions made in recent years by Williams and his associates (*e.g.*, Williams 1942, 1946; Sanborn and Williams 1950) in the field of insect diapause and metamorphosis bring to mind certain common freshwater crustaceans which might be used in similar research programs. These are *Cyclops bicuspidatus thomasi* Forbes and *Canthocamptus staphylinoides* Pearse, each of which has an encysted resting stage apparently comparable to diapause as seen in some hexapods. Although these forms fall far short of moth larvae as experimental material, they nevertheless pose some puzzling problems, the answers to which must be found ultimately in the laboratory.

Encysted *Canthocamptus staphylinoides* were reported first from Douglas Lake, Michigan by Moore (1939), and later from Connecticut by Deevey (1941). The cyst stage of *Cyclops bicuspidatus thomasi* was noted by Birge and Juday (1908) in Wisconsin lakes, and by Moore (1939) in Douglas Lake. The present writer has studied the life cycle of this species in Crystal Lake, Minnesota, where the cyst stage occurs, and has had an opportunity to collect and examine the Douglas Lake *Cyclops* and *Canthocamptus* cysts.

The cysts of both species sometimes occur in tremendous numbers in fine-grained profundal sediments, from which they may be separated by employing an 80-mesh sieve. Active individuals may be found in the collections with the cysts. In the case of *Canthocamptus* these are full grown, but sexually immature. They are negatively phototaxic, thus facilitating their capture, and removal from the sediments. Each cyst contains an individual in the same full-grown stage. On the other hand the *Cyclops* become encysted in the 4th copepodid stage, and the active individuals found in the sediments with the cysts are also in this instar. At this time they have 10 antennal segments; the first four swimming legs have two-jointed exopods and endopods; the 5th and 6th legs, and the furcal rami resemble those of the adults. Two more moults are necessary for the attainment of adulthood, but no moulting or apparent development takes place within the cyst.

Both species occur in anaerobic water, where other entomostracans rarely, if ever, are taken. During the summer all the *Cyclops bicuspidatus thomasi* in Crystal Lake, Minnesota, are benthic, in the 4th copepodid stage, and most of them are encysted. Except for a few in the deeper sublittoral area they are present in anaerobic profundal sediments at the time there is a conspicuous concentration of H_2S in hypolimnion waters. Also during winter stagnation, when the sediments contain a great many *Cyclops*, most of them are in the deeper part of the lake in anaerobic water. They are then active, but still in the 4th copepodid stage. Moore (1939) reported a similar summer distribution for *Cyclops* cysts in Douglas Lake, and both he and Deevey (1941) found *Canthocamptus staphylinoides* abundant in anoxic sediments. A study of these species might start to advantage with an investigation of their respiratory mechanisms.

A few inconclusive experiments have been performed by the writer using these two copepods. First it was discovered that *Cyclops*, excysted no more than one day, remained active for several hours in a strong solution of NaCN. These were from Crystal Lake cysts collected in October, 1948, and it is believed they had been encysted since early June. Their deaths, which occurred overnight, may have been due to osmotic factors. The molarity of the solution, although not determined, was known to be great. More cysts were collected immediately, and ten were placed in a solution of .001 Molar NaCN. Seven of these copepods excysted and six of them lived for two weeks in the solution. Ten others which had been excysted for 10 days succumbed to the same solution within three hours and 20 minutes. Using several other individuals, including some excysted for about a month, it was found that there was increasing cyanide sensitivity with length of time since excystment, although all were in the 4th copepodid stage. With other respiratory poisons (NaN_3 and iodoacetic acid) sensitivity was also directly proportional to time out of the cyst. However, a solution of .001 Molar NaF seemed to have no effect in inhibiting excystment, and did not harm individuals excysted more than 24 days. In the spring of 1949 it was discovered that planktonic *Cyclops* in the 4th copepodid stage just prior to encystment were extremely sensitive to the cyanide solution.

Although admittedly based on extremely flimsy evidence, and poorly controlled experiments, this suggests the phenomena described by Williams and Sanborn (1948) in the cecropia silkworm. During diapause this insect is insensitive to cyanide, but with a termination of diapause a larger fraction becomes cyanide sensitive, and oxygen consumption proceeds.

This evidence of cyanide resistance seen in 1948 has not been duplicated with *Cyclops*. Cysts collected from Crystal Lake in midsummer 1949 were killed by the cyanide solution. Furthermore, those taken from the profundal sediments of Douglas Lake during August, 1950, were killed by a .001 M solution of KCN, and only two out of 25 cysts survived a .0005 M solution more than a day. One of these died after 10 days without excysting. The other emerged from the cyst four days later than did con-

trols in tap water, and died within an hour when placed in a new solution one day after excystment. Out of many tested individuals from Douglas Lake it was found that those emerged less than a day lived only about an hour in the .001 Molar solution. Those emerged for 11 days died in less than half an hour.

None of the Douglas Lake *Canthocamptus* cysts survived in .0005 Molar KCN, although several apparently died part way out of the cyst coat. The active *Canthocamptus* taken from anoxic sediments usually survived 3 or 4 days in the same cyanide solution, but their activity was greatly reduced after 2 or 3 hours, and they simply lay at the bottom of the container twitching their antennae until death. This survival time was much greater than that of planktonic copepods and Cladocera, which died after 15 or 20 minutes. The planktonic species studied were *Cyclops vernalis, Mesocyclops edax, Diaptomus oregonensis, D. minutus,* and *Epischura* sp.

The resting stage is not invariably a part of the life cycle of *Cyclops bicuspidatus thomasi.* Birge and Juday (1908) found that in certain Wisconsin lakes the summer populations remained active with no encystment. Ewers (1930) described its development from egg to adult as taking about 4 weeks when cultured in the laboratory, and she mentioned no cyst.

The factors inducing encystment are not clear. Moore (1939) has suggested a responsible factor or combination of factors in the hypolimnion of Douglas Lake, because the cysts are almost entirely confined to the profundal sediments. In Crystal Lake, Minnesota a few occur in the deeper sublittoral zone as well as the profundal, and the first new cyst observed in 1949 was found during the spring overturn when all depths were well oxygenated. Birge and Juday (1908) found cysts abundant in early summer while the dissolved oxygen content was still high in the hypolimnion of Lake Mendota. These authors listed 6 Wisconsin lakes where the cysts were found. Three of these had an abundant summer oxygen supply in the deep water. In Lake Winnebago, a large, shallow, nearly homothermous body of water, there were many encysted *Cyclops,* while in a similar lake (Sand Lake) the *Cyclops* remained active all summer. Dr. Clarence Dineen has informed me that he found encysted *Cyclops bicuspidatus thomasi* and *Canthocamptus staphylinoides* in the sediments of a shallow pond near Minneapolis. This was during the summer of 1949 when the water was saturated with oxygen, water temperature was about 20° C., and there was no free CO_2 present during daylight hours. The entire pond was essentially littoral. There is some evidence that *Canthocamptus* also encysts in Walden Pond, a deep lake whose hypolimnion contains some oxygen (Deevey 1942).

Deevey (1941) attempted unsuccessfully to induce encystment by exposing *Canthocamptus staphylinoides* to anaerobic conditions. The writer tried the same with *Cyclops bicuspidatus thomasi.* The specimens were taken from the spring plankton of Crystal Lake a few days before the entire new generation migrated to the bottom deposits and encysted. They were all in the 4th copepodid stage. Several *Cyclops* were stored at 10°, 15°, and 20° C. in tightly stoppered bottles containing lake water and a layer of profundal sapropel. Controls were left in unstoppered bottles. At the end of ten days each bottle was examined, and a test for dissolved oxygen was performed. Very few active copepods were found in any of the anaerobic bottles, and none survived at 20° C. except in the aerated bottle. A few cysts were found in all the bottles except the anaerobic one at 20°, and no conclusions could be reached concerning the effects of anaerobiosis or temperature in inducing encystment. Prior testing had shown that anaerobic conditions were established very rapidly in the stoppered bottles. Therefore the animals were subjected to a severe and sudden change, probably not comparable to lacustrine events.

The observations of the writer on the encysting *Cyclops* in Crystal Lake, and those of Birge and Juday (1908) in Lake Mendota have shown the effects of temperature changes on natural encystment to be obscure.

Lucas (1947) has reviewed the ecological effects of external metabolites on planktonic populations. It is possible that the factors inducing encystment are of this type. Perhaps the depletion or reduction of some trace element or compound in the aqueous environment plays a part. Such phenomena might account for resting copepods in shallow ponds and homothermous lakes where temperature, O_2, CO_2, and pH values are far different from those of stagnant hypolimnion waters.

The factors bringing about excystment, especially in natural populations, are also obscure, although it can be induced in the laboratory simply by placing the cysts in fresh water. In both *Canthocamptus* and *Cyclops* excystment then occurs in from one to 4 days, and temperature seems to have no effect. Deevey (1941) discovered that an oxygen deficiency inhibits emergence of *Canthocamptus* for at least ten or fifteen days, but after 5 months in an anaerobic environment the copepods excyst anyway. This is also true for *Cyclops.* Closed vials filled with sapropelic ooze and stored in the dark at 10° C. from July 14 to September 21 were found to contain many active, immature *Cyclops* when examined on the latter date. A few living cysts were

also present. Each vial gave off a strong odor of H_2S, and it is believed the cysts had been in an anaerobic medium during most of the storage time. The factors inducing natural excystment have not been determined. The Lake Mendota *Cyclops* excyst before the fall overturn (Birge and Juday 1908), and the Douglas Lake animals apparently excyst during the overturn (Moore 1939). In Crystal Lake some excystment commences a month before the fall overturn, although many cysts remain well into January. Most of the *Canthocamptus staphylinoides* of Douglas Lake also excyst at the overturn (Moore 1939), but Deevey (1941) found that 97% of the total population of this species was still encysted as late as December in a Connecticut lake. Obviously copepod populations in different environments behave quite differently.

In Crystal Lake a large portion of the *Cyclops bicuspidatus thomasi* population lives a little more than a year, of which about 10 months are spent in the 4th copepodid stage. Most of the reproduction occurs during the spring overturn when the entire population is planktonic. Apparently the life cycle of this species and that of *Canthocamptus* in Douglas Lake is also an annual event. Deevey's observations on *Canthocamptus* in Connecticut suggest the same thing. However, in Dineen's Minneapolis pond the entire population of *Cyclops bicuspidatus thomasi* excysts in midsummer and there is a second generation produced while the nearby Crystal Lake population remains benthic and encysted.

Coker (1933) reported the case of a species of *Cyclops* from a pool in Chapel Hill, N. C., which developed from egg to 4th copepodid stage in 24 days or less. Development ceased at this stage for as much as 143 days, during which time the animal remained active. The 5th copepodid stage and adulthood, ending in death, required only about 76 days. This long period of arrested development could be terminated by subjecting the *Cyclops* to low temperatures. The state of arrested development at the 4th copepodid stage in the Chapel Hill *Cyclops* is but a short step from the arrested development and arrested activity of the encysted *Cyclops bicuspidatus thomasi*.

From the evidence so far it appears that copepod encystment may or may not be a feature of the life cycle, and that environmental factors, although obscure, must play a part in initiating and terminating the encystment. It is a state of dormancy occurring during the ontogeny of the individual, but is not comparable to the physiological activity which takes place during insect pupation as the imago is being formed. It is probably a period of little physiological activity, which terminates with an organism apparently unchanged morphologically from the original condition. On the whole, the phenomenon appears to parallel insect diapause.

Summary

In some natural populations of *Cyclops bicuspidatus thomasi* and *Canthocamptus staphylinodes* the ontogeny of each species includes an encysted resting stage within a definite instar. The factors inducing encystment are obscure. The presence or absence of the resting stage in a population can not be correlated with lake typology or with any of the obvious environmental physicochemical conditions.

Excystment can be induced by placing cysts in oxygenated water, yet natural excystment does not necessarily coincide with lake overturn periods. Excystment is inhibited temporarily by an anaerobic medium, but the copepods emerge eventually in such an environment.

Both species survive long periods in anoxic sediments, and are believed to be capable of anaerobic respiration. There is limited evidence that *Cyclops* is resistant to respiratory poisons during part of the resting stage, and may retain the resistance for at least two weeks after excysting, if kept within the poison solution. Newly excysted individuals in an aerobic medium become increasingly susceptible to respiratory inhibitors as time passes even though in the same instar. Active *Canthocamptus* individuals from profundal sediments are paralyzed by cyanide, but survive 3 or 4 days in a solution which quickly kills planktonic copepods of other species.

Physiological and ontogenetic features of copepod encystment suggest that it may be defined as diapause, a word which has been applied in most cases to insect phenomena.

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A SURVEY OF LITERATURE ON FUNGUS SOCIOLOGY AND ECOLOGY—II

Many papers have been published dealing with the autecology of the fungi, especially pathogenic fungi, such as those on weather relations summarized by Foister (1929, 1935, 1946). Texts on plant pathology (Heald 1932) and forest pathology (Baxter 1934; Boyce 1938) as well as texts on fungus physiology (Lilly & Barnett 1951) also list large numbers of such papers and the literature of phytopathology is made up almost exclusively of such studies. However, comparatively few papers deal with the synecology of the fungi, especially analyses of fungi as parts of the biotic community in which they live.

The earliest paper attempting to relate fungi to the vascular plants around them seems to have been a two volume book by J. Bolton dealing with the fungi in a portion of Yorkshire, England, published in 1788. One hundred and fifty years later, Grainger (1940) was able to use this in conjunction with a list of fungi of Yorkshire (Mason & Grainger 1937) as a basis for a discussion of the changes of the fungus population of the area. No quantitative data were presented in either discussion although the list was based on collections made in what may be the most intensively collected area in Great Britain if not in Europe, the Northern Hemisphere, or the world.

Ferry is usually cited as the first to relate fungi to the type of substratum upon which they grow. In 1887, he listed species found on needle-leaved (conifer) litter and broad-leaved (oak, beech, etc.) litter, and in 1892 he listed species of calcareous and of sandy soils. In 1901, Maire, Dumee, and Lutz presented a list of the fungi of Corsica in which they listed fungi by plant association and type of soil on which they were found. Boudier (1901) discussed the nature of the soil and the vegetation which grew in Corsica and their effect on the development of the fungi found there. R. Scharfetter (1908) discussed some of the relationships between the fungi of Villach in Silesia and their environment. He presented a number of observations on methods of spore dispersal and grouped those fungi found associated with forest types, tree species, grasslands, compost and dung, those which fruited underground, and those which were considered saprophytes.

Jakob Lange (1923), in Denmark, emphasized that there are ecological relationships among the fungi and between the fungi and the other organisms of a community. His ten pages of discussion appear to have been the inspiration of many more recent workers for his notes are cited by many of the writers who will be mentioned below. Ramsbottom (1926) described methods he considered fundamental for students of fungus sociology and for students interested in correlating the fungus and vascular plant populations of a region.

In the only book on mycoecology known to the writer, Gilbert (1928) elaborated on the notes of Lange and the suggestions of Ramsbottom, adding a few ideas of his own, citing examples of the type of work which can be done, and emphasizing the need for further work in the field. So far as can be found, no one has actually followed the system of study and analysis suggested by Ramsbottom and Gilbert.

Krieger (1936) indicated in some introductory remarks to his "Mushroom Handbook" that fungi differ among themselves as to nutritional requirements, periods of seasonal development, etc., and gives one of the few charts published in North America on the seasonal distribution of the fruiting of the common edible and poisonous species. Recently, Murrill (1949b, 1949c) has given comparative dates of fruiting of species in certain genera of agarics where records are available from his collections in Florida and from those of Kauffman in Michigan. These are averages based on two entirely different sets of year-periods separated by more than 20 years.

One of the earlier studies in the synecology

of the fungi appears to have been that of Graham who in 1927 made a qualitative study of the ecology of the fungi of the Chicago region. He indicated something of the habitat requirements, seasonal distribution of fruit bodies, and types of fruit bodies to be found, and gave some quantitative data on the distribution of the fruit bodies in one location.

Hruby (1928) listed the fungi of Moravia and Silesia, associating them with the host on which they grew and the host communities. His system was very complex and did not take into consideration the separate physiology of the two types of organisms. In a second study from the same area, Canon and Plitt (1939) listed the Basidiomycetes of the Iglauer Berglandes placing some emphasis on the plants and associations with which fungi were found associated.

P. D. Fehér (1933) has produced one of the few studies on soil micro-organisms in which bacteria, micro-fungi, algae and protozoa were studied from the same area and their activities reported simultaneously. The larger fungi, the lichens, liverworts, and mosses were excluded from this study. Quantitative studies of soil activities by micro-organisms is usually carried out on the basis of the number of thousand, ten thousand, hundred thousand, or million organisms plated out in the laboratory per unit of soil sample. Fehér uses this technique but in addition presents a systematic report on the organisms found in which it was indicated that although 66 species in 36 genera were isolated, it was species of *Aspergillus, Penicillium,* and *Mucor* that were dominant. This was shown by means of percentages and reports of species isolated. The studies were carried out in areas from latitudes of Hungary at 47°47′ N. to those of northern Finland at 69°30′ N. It was found that the pattern of fungus-actinomycete-bacteria distribution usually found in temperate regions pertained in the more southern latitudes while in the north the numbers of bacteria decreased noticeably. This was attributed to the colder temperatures. Although the numbers of bacteria decreased to the north, the numbers of fungi did not decrease proportionately, so that the ratio of fungi to bacteria increased as more northerly latitudes were reached.

Fehér introduced four ratios of interest to future workers with soil organisms: the ratio of bacteria to fungi in the soil expressed by the result of dividing the number of bacterial colonies by the number of fungus colonies produced with normal isolation techniques; the ratio $p_1 \cdot p_2$ in which p_1 is the percentage occurrence in relation to the study area and p_2 is the average percentage of the percentage occurrence on the single study area; and the two R factors: R_1 being the soil moisture value expressed as a percentage × soil temperature value; R_2 being the precipitation × air temperature. It may be mentioned that R_1 is the R-factor used by Ubrizsy in a later paper and rather than being referable to soil humidity as is done by Fehér's students, is only another way of presenting incomplete data.

Williams (1936), in a study of the *Fagus grandifolia-Acer saccharum* climax in northern Ohio, listed a number of fungus species but did not compare these with the fungi to be found in other forest types in the area nor did he analyse the fungus populations quantitatively.

Baxter (1937) found that in forest plantations in Michigan, introduced trees were more susceptible to invasion by various pathogens here than in their native habitats in most cases. Definite fungus succession patterns could be established depending on the tree species. Such attacks by fungi were sometimes of minor importance, but in other cases so important as to prevent the establishment of tree species on certain sites.

Mason and Grainger (1937) presented a "Catalogue of Yorkshire Fungi" in which fungi collected between 1881 and 1935, on forays of the Yorkshire Naturalists Union and otherwise, were enumerated systematically and in which the populations of the 5 vice-counties were compared. The following number of species in the different classes of fungi were obtained in each vice-county:

Class	Vice-county					Whole county
	61	62	63	64	65	
Myxomycetes	75	99	83	105	56	138
Phycomycetes	18	52	49	46	36	83
Ascomycetes	185	580	466	284	236	849
Basidiomycetes	693	1,588	1,199	1,038	723	1,969
Fungi Imperfecti	55	233	193	159	69	422
Total	1,026	2,552	1,990	1,632	1,120	3,461 spp. 654 gen.

One hundred and forty locations in the county were visited in addition to those visited during the forays. Also recorded are 356 visits to the county by groups other than official forays. No attempt was made to explain the difference between the small number of species collected in V-C 61 as compared with the nearly 2.5 times larger number collected in V-C 62. No attempt was made to correlate findings with seasons, soil types, plant communities or other features, whether disturbed or undisturbed, throughout the period of study. Gaps occur in the list as apparently no serious attempt had been made, up to that time, to isolate such groups of species as soil fungi, predacious fungi, chytrids, water molds, etc. The list is overbalanced by fleshy and woody fungi which shows in part the special interests of most of the people who have collected in the area.

Malençon (1938) has reported on the fungi found in the Middle Atlas of northern Africa in the vicinity of Azrou. While his work lacks the methods of quantitative synecology, his observations on the fungi associated with the three vascular plant associations in the region are of interest. The principal associations are each dominated by one species: *Quercus ilex, Q. faginea,* and *Cedrus libanotica* ssp. *atlantica.* Each of these trees is considered to have an influence on the flora and the mycobiota which accompanies it. In the coastal plain region of Morocco, two seasons are represented in particular: a cool humid winter, and a hot dry summer. Here forests of *Quercus robur* support a fungus population somewhat reminiscent of the deciduous forests of central Europe but including more species of the warm temperate or steppe regions of the world. In addition to these two seasons, in the Middle Atlas, probably because of the higher altitudes, the winters have lower temperatures with snow, and with brief autumn and spring seasons. The expected similarity to the forests of Europe, so far as fungus populations are concerned, is counterbalanced by the long, hot, dry period of the summer. Where comparisons are made between the forests of the Middle Atlas and those of southern Europe, groups of species including whole genera characteristic of the European forests are absent. The severity of the climate is somewhat modified in the case of the *Quercus ilex* forest by the presence of thickets of *Ilex aquifolium,* and in the case of the *Quercus faginea* forest by the fact that this association occurs in an area characterized by springs, the fog belt, and slopes of shaded ravines. In the area of *Cedrus* forests, the climatic conditions and the conditions of the forest floor, where little litter occurs, combine to give a rather poor fungus population.

In 1939 and again in 1947 Baxter published results of studies made in Alaska on successional patterns of fungi in certain natural plant communities which were either established or were being developed on new sites such as river bars and volcanic areas. In mature forests, he studied transects 100 chains wide and several miles long emphasizing only those fungi associated with forest trees, shrubs, and herbs. He found a degree of host specificity in such fungi. Where a series of hosts occur together in one association, a series of fungi occurs with them. These fungi extend into other associations only where their hosts penetrate into, or remain as relicts in, these associations. In the valley of the Yukon River, where Baxter worked on the river bar sere, *Picea glauca* seems to be the climax dominant, preceded on young terraces by *Salix,* then *Populus* stages. The rate of succession is speeded up by various rusts, cankers, and wood rots which eliminate *Salix* more quickly than if the plants remained healthy. The eruption of Mt. Katmai on Kodiak Island was found to have eliminated alternate hosts of certain heterocyclic rusts, thus tending to increase the health and vigor of forest tree species until the alternate host reinvaded the area.

Slipp (Slipp and Snell 1944) found that it was possible to correlate the species of the Boletaceae with the different stages of forest succession in one sere in the forests of the *Thuja-Tsuga* zone in northern Idaho.

The work of Karl Höfler and his students initiated in Austria just before the outbreak of World War II has been discussed as has that of Haas (1933) by Cooke (1948).

Friedrich (1942) returned to the Oetz Valley in 1941 and spent several weeks studying the fungi and the climatic conditions under which they occurred. Along this valley are subsidiary valleys, forested slopes, and glaciated valleys in timberline areas, so that a number of habitats were selected for study from the valley floor at 1,036 m. to 2,600 m. in the alpine boulder fields and snow valleys. The study is qualitative since time was not available for quantitative studies except for the collection of macro- and micro-climatic data. Species of fungi found in each habitat are listed and some discussion is presented for each group of species in relation to their habitats and their restricted or ubiquitous distribution elsewhere.

Lind (1940), working in northern England, found a correlation between numbers of individuals of fruit bodies and the vegetation and soil types studied. Also working in northern England, Mary Grainger (1942) indicated the possibility that nitrogen was the controlling factor in fungus fruiting since, according to the techniques she used, nitrates and ammonia were present in minimum quantities in the summer, and only in autumn were high amounts of available nitrogen, temperature, and soil moisture

present in sufficient quantity for fungus fruitbody production.

In 1943, Frei-Sulzer suggested a new method for obtaining quantitative data on fungus populations. This included visiting the sample area every two days, gathering and weighing the full grown specimens. Young specimens were not to be disturbed and observations should be continued over a period of several years.

At Oxford University in England, W. H. Wilkins and his students initiated a series of examinations of beech, oak, and pine woodlands, adjacent grasslands and heaths to determine the relative abundance of species of fungi in these habitats with reference to vegetation cover, temperature, precipitation, and soil types. The studies, which were undertaken before World War II at about the time Höfler's students were studying similar problems in Austria, resulted in the publication of five papers between 1937 and 1946.

Wilkins, Ellis, and Harley (1937) were interested in the fungus flora-vascular community relationship and in this report they ignored all other considerations. Stations were selected for homogeneity of vascular community in oak, beech, and conifer woods, grasslands, and *Calluna* heaths. Stations were of a size (not stated) which could be examined by 12 to 20 people in a day, specimens were collected in the field and determined and listed in the laboratory. The study was made over a 5 year period near Oxford and Haslemere, England. Constancy of species and "frequency" (number of fruiting bodies on the plot) of individuals were emphasized in the results of the study. Only one plot was established in each of the 5 communities. It was found that 14 species occurred in all 5 associations, although over 630 species were studied. It was found that in each community one-fourth to one-tenth of the species were exclusives. However, each community was shown to have a characteristic fungus flora, although many species overlapped into one or more of the other communities, by means of lists of the principal species found in each. Factors affecting the observed "frequency" of individuals in a community included period of observation in relation to the fungus season, weather conditions at the time of examination, and actual seasonal periodicity of the individual species. Comparisons of the fungi in the vascular communities in relation to each other were made by means of tables and species lists.

Wilkins, Harley & Kent (1938) studied the fungi of Charlton Forest, Sussex, England. The forest was divided into 4 somewhat homogenous stations each of which was treated in detail as to its phanerogamic vegetation and fungus population by means of "zig-zag" transects, a method of studying a large area by wandering through it randomly in a zig-zag manner producing an elongate transect (probably never exactly duplicatable). The dominant tree species was *Fagus sylvatica,* with *Quercus robur* and *Fraxinus excelsior* occurring locally. Three principal herbaceous unions formed the basis for segragating the fungus population. Depth of humus and leaf litter were recorded, soil texture was determined by handling the soil dug from holes in the plots. Six species of mosses were found on the ground throughout the forest. The 132 species of fungi were tabulated according to their relative abundance in each of the three herbaceous unions, in relation to soil types found (heavy, light, and rendzina), in relation to humus, leaf litter and wood present, in relation to depth of "humus" (duff), and in relation to pH. Because of incompleteness of the list of fungi, imperfections in indication of frequency, great variation between number of individuals and the small number of species with high "selective frequency," the results were considered inconclusive and generalizations could not be made from them.

Wilkins and Patrick (1939) studied 20 grassland stations near Oxford, Leicester, and Haslemere, England, on chalk, clay and sand soils. Soil profiles, texture, organic matter of the upper two inches, pH of the upper one inch, and floristic composition were recorded. Lists of fungi were made every two weeks in the autumns of 1936 and 1937 by the zig-zag transect method selecting a transect route which necessitated spending at least 3 hours in each plot at each visit. "Frequency" (number of individuals in the plot) was estimated and recorded by means of symbols in the field. In 1936, 147 species of fungi were recorded, 125 species were listed in 1937, and of those, 100 species were found in both years. The seasons were relatively cold and dry. Species typically growing near a tree, or stumps, or on wood were excluded from the lists. *Hygrophorus virgineus* was the only species found in all 20 stations. Constancy was related to soil types with lists of species characteristic of each soil. "Frequency" of individuals was discussed under several units based on number classes of fruit bodies such as more than 2,000, 2,000–1,500, 1,500–1,000, 1,000–500, 500–50, 50–10. "Frequency" and constancy were compared, "frequency" was related to soil type, and species lists correlating these factors were presented. "Frequency" and constancy in certain fungus species on all stations were compared in relation to: species with relatively equal distribution, species with relatively high constancy on chalk and sand, on clay and sand, on chalk, and on sand.

Wilkins and Patrick (1940) studied three chalk, clay and sand grassland stations near Oxford, England, at intervals of 12–16 days

from 1 January 1937 to 1 January 1938. In each station, a quadrat 100 yards on a side was laid out. At each visit the temperature, precipitation, water content, and pH of soil were measured and the fungus species and individuals were determined. Temperature was recorded by means of maximum and minimum thermometers placed on the ground under screens; the variation between stations was negligible. Rainfall was measured by rain guages placed on each quadrat, but it was found that the fungus vegetation was affected more by the water content of the soil than by rainfall. Water content of the soil was determined after each visit on mixed random samples and was expressed as per cent of the fresh weight; it was found to vary throughout the year with the soil type. pH was taken at each visit and the mean was found to be: chalk 7.0, clay 6.1, and sand 4.9. Fungi were observed by the zig-zag transect method and at least one species was found on each visit to each plot except in mid-August, when the water content of the soils was lowest. To show graphically the relation of maximum-minimum temperatures, water content of soil, and fruit body numbers, composite charts were presented for each station with a summary chart using the averages for all three stations. Seasonal distribution of individual species was given by means of a table indicating the numbers of fruit bodies found at each visit throughout the year. Figures for total fruit bodies were found to be inflated in seasonal summaries by certain species which produce large numbers of fruit bodies. Fungus fruiting was apparently conditioned by environmental factors, but the authors were hesitant to say which or how.

Wilkins and Harris (1946) laid out quadrats 100 yards on a side in a beech (*Fagus sylvatica*) wood and in a pine (*Pinus sylvestris*) wood. They gave thorough ecologic characterizations of both sites. At weekly intervals, except in the "depth of winter," fungi were counted and temperature and precipitation were measured. As a check, temperature and precipitation were recorded in a nearby heath. At each visit, the fungi were collected, counted, recorded, and destroyed. Rain guages were set up in each quadrat. Temperature was obtained at the ground surface and 3 inches below, the former presumably affecting the emerging fruit bodies, the latter presumably affecting the growing mycelium and the developing sporophore initials. Samples of the surface litter dropped during the current year, the lower litter down to 3 inches dropped the preceding seasons were taken, their water content determined, and expressed as per cent of fresh weight. Density of the canopy was estimated in comparison with the light in an open heath by means of a light meter. Thirty-six species were studied in the beech-wood and 24 in the pine-wood. Tables were used to show the seasonal distribution of fungi in both habitats. Charts were used to show the relationship of the amount of canopy during the year, the amount of rain received on the surface of the canopy, and the temperature both outside and inside the woods. Graphs were used to show the relationship of rainfall, temperature, and water content of the substratum. Finally, a combined graph shows the numbers of fungi in relation to the temperature and water content of the substratum. These data indicate that there was a lag of about two weeks between the time of maximum temperature and that of maximum fruiting in the pine woods, and of about three weeks in the beech woods, the per cent of water content of the litter layers increasing somewhat continuously during this season. That more fruit bodies were produced in the pine-wood with canopy than in the beech-wood without canopy in the fall and early winter was attributed to the effectiveness of the canopy. The lag between maximum temperature and maximum fruiting, and the duration of fruiting period, varies from species to species as is indicated by species lists.

The work of Wilkins and his students is characterized by the presence, in the vicinity of the studies, of a herbarium containing nearly complete series of identified species of fungi in the area, and by a refinement of technique during the study period especially in the use of the "zig-zag" transect method of plot study.

Bässler (1944) studied the fungi which appeared in a number of stands of *Castanea sativa* Mill. in the state of Pfalz in southwest Germany. This species was first brought to northern Europe by the Romans and has since been maintained as a fruit, forest and timber products tree. Sixteen stands were studied on one to four occasions and from each stand data similar to those obtained by Haas (1933) were presented. It was found, with the techniques used, that throughout the year in the several areas the pH of the soil varied from 3.8–6.4. Collections were made of 275 species of fungi of which 219 were definitely associated with the chestnut; of these 182 grew in the soil, 29 on wood, and 9 on either soil or wood. However, Bässler could not find any species of fungi exclusive to the chestnut woods which could not be found in other woods. At least 3 species were ubiquitous, and 18 species not characteristic of chestnut woods were present in these woods. Fungi, as well as herbaceous undergrowth, appeared to be of the species characteristic of acid rather than neutral or basic soils. Of the species typical of chestnut woods a number extended into adjacent conifer forests. It is thought possible that the chestnut woods have replaced oak woods since the fungi present are more characteristic of oak than of other forest

types represented in the region. Many fungi typical of beech, and most fungi typical of birch, aspen, alder and willow woodlands are absent. Most of the species fruit in late summer or fall, the species which usually fruit in the spring being characteristically absent.

Species of the genera *Amanita, Tricholoma, Lactarius, Russula,* and *Boletus* were selected for special study. It was found, for instance, that in these genera the following species proved to have the highest constancy values: *Amanita mappa, A. rubescens, A. vaginata, Tricholoma saponaceum, Lactarius camphoratus, Russula cyanoxantha, R. densifolia, R. emetica, R. foetens* ssp. *laurocerasi, R. fragilis, R. vesca, R. lepida, Boletus edulis,* and *B. miniatoporus.* In 4 study areas during 1942, the productivity of certain species of these genera was studied. In the first third of August a high point was reached with a total of 343 specimens (specimens being individual fruit bodies of any species), in the second third of September following an extremely dry period a low point was reached with 18 specimens. A second high point was reached in the last third of October with 249 specimens. Stand surveys with regard to sociability and abundance indicate that certain species of one genus are replaced by others of the same genus during the season. As the season progresses, *Russula fragilis* replaces *R. emetica, R. nigricans* replaces *R. densifolia,* and *Lactarius vellereus* replaces *L. piperatus.* It was found that *Amanita rubescens, Russula cyanoxantha* and *Boletus miniatoporus* fruit in a soil moisture of 5% to 20% measured at 5 cm. depth. *Russula lepida* and *R. virescens* fruit in a soil moisture of 4.4% to 6.4%, and it is thought that they are thus especially resistant to dryness in the soil. As in all European work of this type seen to date, moisture percentage was determined directly on field samples by obtaining the percentage of moisture in a given soil sample without regard to comparison with wilting coefficient or field carrying capacity of the soil in question. The technique may be refined by averaging the results of several samples from the same soil type. At least 3 species in the Castanetum do not show a preference for a pH range. The pH was measured for soil collected with fruit bodies of these fungi throughout the period of their fructification and this was found to be for *Amanita rubescens* 3.7–6.3, for *Russula cyanoxantha* 4.3–6.4 and for *Boletus miniatoporus* 3.7–6.3.

In Yorkshire in northern England, John Grainger (1946) and several members of the Yorkshire Naturalists Union have become interested in the study of mycoelogy. In addition to the comparison which he drew with Bolton's work (1940), Grainger has contributed some new studies on the ecology of the larger fungi. He was particularly interested in the effect of the pH of the substratum, the effects of the amount of water and organic matter in the substratum, and successional and phenologic changes in the fungus population. Methods used in the enumerated studies were non-critical and the results not too satisfactory. However, his sociologic studies resulted in some figures which indicated that disturbance of the habitat resulted in a change of the number of fungi fruiting. This was attributed to a change in the water holding capacity of the soil. In the phenologic study, he commented on the fact that certain fungi, such as *Agaricus campestris,* fruit at any time in culture, whereas in nature fungi have certain periods during which they fruit in greater abundance. He explained periodic fruiting as a result of the occasional concomitance of the required temperature, rainfall, and available nitrogen.

In 1946 Zaleski *et al.,* published a list of fungi found in certain government forests in Zielonka, Poland. They described the forest types studied, listing some of the climatic and soil characteristics and gave 4 abundance classes for the fungi found. These abundant class concepts were apparently developed independently of other workers and were based on estimated rather than counted fruit bodies.

Results of a study of a raised *Sphagnum* bog in north Zealand in Denmark were published by Morten Lange (1947). Between 1942 and 1944, 69 visits were made to the area during which time 204 species of fungi were enumerated in the 40 acre bog area. Eleven types of habitat independent of trees and 12 types dependent on trees were discussed. Meter square permanent quadrats were placed so that habitats dependent on and independent of trees did not overlap. Counts were made at least twice a month in each quadrat and included all individuals whose stipes occurred in the quadrat. Fruit bodies were not collected unless absolutely necessary for identification purposes to prevent damage to the mycelium, either directly or through the introduction of parasitic organisms to the mycelium. Specimens within one meter of the periphery of the quadrat were counted separately if they occurred in the same association. (Unless one is thoroughly familiar with the mycobiota of an area this technique is not usable since many specimens are required for identification purposes in the laboratory by the worker or his correspondents. In addition to being a systematic mycologist in his own right, M. Lange's father, Jakob Lange, was a famous student of the Agaricaceae of Denmark and Europe as well as of North America.)

Precipitation and temperature data were obtained from a local meteorological station. The highest precipitation was received in August and September. A lag of three weeks oc-

curred between this time and the period of maximum development of fungus fruiting. pH of the peat varied between 3.7 and 4.2. Water content of the substratum and insolation were not measured.

In summarizing the development of the agaric flora throughout the growing season, overlapping curves based on the distribution of fungi in 102 quadrats, average species density per quadrat, and average density of individuals per quadrat were used. It was found that in each year these curves were very similar. The maximum development occurred in October with a secondary peak in June or July.

Thirty-three common species were compared on a chart and it was found that several "aspects" could be distinguished: (1) *winter,* at least two species fruit during thaws; (2) *vernal,* late April to early May, if delayed by a late season this merges with (3) *pre-aestival,* end of May to early June, mostly sphagnicolous species, number of species increasing; (4) *aestival,* July to early August, fleshy species increasing although severe drought may eliminate all species; (5) *autumnal:* (a) *early autumn,* late August to early September, increase of species; (b) *mid-autumn,* late September to October, largest number of species and individuals; (c) *late autumn,* late October to November, thinning out of species.

A comparison was made between several of the habitat types in this bog and similar ones in other bogs in northern Denmark.

In evaluating some of his own techniques, Lange indicates that a mycelium may not fruit each year. It may fruit outside a quadrat one year and inside the next, and the opinion is expressed that a three year study is inadequate for generalizations. Based on constancy percentage results, the sampling technique seemed adequate for this bog. Slightly larger quadrats would have been better, but more than 10 quadrats would not be practical in most areas. In summer and during the autumn, day to day observations should be made for a quantitative study of the fungi. For a qualitative study of the fungi in relation to the vascular plant or sphagnum communities, fewer observations are required. One observation can give as high as 50 per cent of the fungus species, 4 observations can give 80 per cent accuracy, while 8 observations can give 85 to 97 per cent accuracy.

During a 15 year period, Jules Favre (1948) studied the fungus biota of 65 raised bogs in the Jura Mountains of Switzerland. He made a total of 200 trips visiting some bogs as often as 26 times in all parts of the growing season between April and October. Four hundred eighty-five species were listed. On each trip all species observed were collected. Sample plots were not used but Favre felt that his method was satisfactory since he believes that a fungus may be a "characteristic" species of a vascular association even though it appears sporadically.

In these Jura bogs, ecological conditions were briefly summarized: "climate very harsh, strongly and relatively constantly rainy, soil with maximum humidity, poorly aerated and oxygenated, minimum (3%) of mineral and nitrogen nutrition, maximum acidity, minimum bacterial activity."

Each of the 4 principal and 6 subordinate *Sphagnum* and vascular plant associations have their characteristic fungus species. Favre also notes a special fruiting habit for the central stemmed species of agarics. Whether it is because *Sphagnum* continues growth as the fungus fruit body grows, or whether it is because the mycelium is deeper seated than in other habitats, in these bogs the agarics have greatly elongated stipes presenting a much more slender aspect than found in those of other habitats.

There appear to be two important groups of fungi characteristic of the bogs. Twenty-two species are found only in close association with *Sphagnum.* The explanation of their interrelationships is not clear; possibly the fungi are either saprobic or mycorrhizal. Individual fungi in this group fruit in specific seasons and regions within the series of bogs in the area. The second group of fungi includes fungi characteristic of very acid conifer forest soils. Favre felt that at least here fungus distribution is controlled by the chemical composition of the soil, for species of calcareous soils are rare in the bogs although the bogs adjoin such soils. Most of the bog species also found in other habitats occur on very acid silicious soils of conifer forests. A good example of this is furnished by *Amanitopsis vaginata;* the typical subspecies, common on calcareous soils, was found only 5 times in the bogs, whereas subspecies *fulva* was found 113 times in 31 bogs.

Ubrizsy (1948) used Fehér's *R*-factor (the R_1 mentioned above) to explain the qualitative appearance of fungi in oak and fir woods. He considers "*R*-factor" and "soil humidity" as synonymous and indicates that there are two fungus peaks in oak woods, summer and autumn, and one for fir woods, in the autumn. Optimum conditions for fungus growth in an oak wood were found in the summer with a "soil humidity" of 20–30%, and in a fir wood in autumn with a "soil humidity" of 30–40%. Since soil humidity is considered by students of soil science to be 100% when the soil is above wilting coefficient, the terminology of this paper appears to be incorrect.

Pirk (1948), in a paper presented by Prof. Tüxen of Hannover, listed the fungi found in a plot study of two phases of the *Querceto-Carpinetum* in the vicinity of Hannover. Four

plots were set up in the *corydaletosum* phase and 9 in the *asperuletosum* phase. Each study area included 100 square meters of surface and the flowering plants, mosses, and fungi were listed for each giving such data as number classes of fruit-bodies, sociability classes of fungus fruit-bodies, and size classes of fungus fruit-bodies. The fungi are listed either as soil- or wood-dwelling and in the table comparisons can be made between those growing in each of the 13 plots. Prof. Tüxen was astonished at the fact that the table showed that the ratio of fungi to vascular plants was about 3:2 and that there were more indicator fungi than indicator plants as brought out in the study which was made over a period of a year. On this basis, it was thought that in addition to the association, possibly subassociations could be established on the basis of the fungi in a community. Possibly the use of fungi could confirm the distinctness of associations previously established purely on the basis of higher plants.

Scheerpeltz and Höfler (1948) studied the relationship of beetles to fleshy fungus fruit bodies and based their researches on quantitative methods. Their work, published in book form, has been reviewed by Cooke (1951).

W. A. Murrill (1949a) has found that in Florida certain fungi are characteristic of certain forest types. Well-drained areas occupied by *Pinus palustris* and *P. taeda,* the so-called "high pine woods," are the habitat of an entirely different series of fungi than is found in the poorly drained "flatwoods" where *Pinus caribaea* occurs. Even though the areas are burned over annually for improvement of grazing conditions, or logged off and permitted to come up in broad-leaved trees, or planted to *Pinus palustris,* this series of fungi remains upon it so long as adequate litter and humus are maintained. The region is described climatically and a description of the soil, litter, and humus conditions is given. A list of 85 species found in the "high pine woods" (only 7 per cent of the species found in Florida) is given although no list is given for the "flatwoods."

M. Moser (1949) gave an account of his sociologic studies on fungi in burned areas in conifer forests on sandstone near Innsbruck, in the Australian Tyrol. In this work, he found several seral communities of fungi on burned soil. Within 1 to 4 months, a Pezizaceae stage develops characterized by a number of species of Discomycetes, followed by a *Funaria* stage, then a *Bryum* stage, and finally a stage characterized by "nitrate" plants. Each of the stages following the Pezizaceae stage is characterized by certain fungi which are "anthracobiont" (living only on burned material), "anthracophilous" (preferring burned areas but found on other areas), "anthracoxenous" (living on other areas but tolerating burned areas), and finally "anthracophobous" (not tolerating burned areas), Pyrophilous fungi (fungi found on sterilized soil) and anthracobiont fungi are characteristic of the Pezizaceae stage.

Boughey (1949) has attempted to apply certain synecologic techniques to plant pathogens. He lists several difficulties inherent to such a study, difficulties common to such studies of all organisms but more obvious in work with fungi. He restricted his statements to the pathogens of economic plants. To be maintained in an area where outbreaks of a disease can reach epidmic proportions there are 3 critical stages in the life cycle of these fungi: 1. long distance dispersal; 2. weathering-over periods during which the crop is not being cultivated; 3. short distance dispersal. The latter was considered the most critical for the attempted study and on the basis of precipitation alone, it was possible to produce histograms showing the relative distribution of 7 types of plant pathogens in 7 relatively homogenous areas under intensive cultivation from Scotland to Mauritius in the tropics. Rather than an application of synecology this seems to the writer to be a summary of some well-known principles of autecology of plant pathogens.

Westerdijk (1949) proposes that students of micro-organisms become more familiar with the concept "association" for in her work with various organisms which cause decay, spoilage, etc., several associations can be determined. These associations are defined on qualitative bases and consist merely of lists of species isolated at any particular time from various products and substrata. Sixteen habitats of commercial or agronomic interest are considered. If there is any seral relationship between the molds listed for each habitat as indicated by a specific preference for one or another product of the deterioration of the original substrate, this is not indicated.

Duddington (1951) has attempted to apply the methods of vascular plant synecology to the study of predacious fungi in England. The report presented appears to be hardly more than a qualitative study of the habitats in which such fungi can be found rather than a quantitative study of these fungi in those habitats. The use of quadrats in this study was a disciplinary action designed more to restrict the worker to a small unit of area. The materials studied included leaf mold, decaying wood, partly decayed plant remains, dung, and living bryophytes. It was found that more nematodes and protozoans were found in the latter habitats and here the predacious fungi grew more abundantly. This group of fungi deserves more attention and it is hoped that the techniques will be refined so that more information about them can be obtained.

Warcup (1951a) applied quantitative techniques to the study of soil fungi vertically through soil profiles. Five soils in Lakenheath Warren, England, were chosen and 20 profiles were examined in each of these soils. Soil samples were removed at each inch of depth to 8 inches and thereafter at each 2 inches for the remainder of the profile to 30 inches or more where this was necessary. Five to fifteen mg. of soil from each sample were dispersed in agar on a petri plate and the colonies developed after incubation counted and tabulated; dilution plates of 1:5,000 were also used. It appeared that numbers of species and colonies of fungi were influenced by soil texture and soil reaction. Depending on species of fungi, there is a great difference between activity at different levels in the soil as indicated by histograms for certain of the most wide-spread and more unusual species or groups of species encountered. Two sets of data presented may be of interest here:

Soil	A	B	C	D	E
Numbers of species isolated from 20 profiles in each of 5 soils					
Total number of species	48	62	74	79	69
Average number of species per profile	23	33	37	35	25
Number of species from only one profile	6	11	12	17	17
Number of common* species	21	27	33	31	21
Numbers of colonies of fungi in 5 soils (in thousands per gram soil)					
pH of sample	8.0	7.5	6.4	4.2	3.9
Number of colonies	36	59	74	245	425

* A species was considered "common" if it was represented in more than 10 profiles of even one soil.

Sixty-one species were found to be "common" and these were tabulated listing the number of times of occurrence in each soil. Eight of these were present in all 5 soils and one of these was common in all 5 soils. Techniques were described for microscopic examination of the soil for observation of organisms *in situ*. The higher bacteria and fungi were discussed by groups in their relation to the soils studied and *Mucor* and *Penicillium* species were tabulated according to their occurrence in these soils since these genera were represented by more species than other genera studied.

Warcup (1951a) has made preliminary studies of the larger fungi of Lakenheath Warren in connection with the microscopic soil fungi of the area (mentioned above). The larger fungi are listed according to the 5 soil types and pH of each. A chart is presented correlating period of fruiting with precipitation in mm. and per cent of moisture in the soil at 1 inch depth. Thirty-four species of Basidiomycetes were studied. Three of these were selected for more careful studies. It was found that they could, by special techniques, be isolated from the soil and the area in the soil occupied by the mycelium studied. The direction of growth of the general mycelium through the soil was determined, as was the percentage moisture of the soil throughout the mycelial zone. The mycelium was found to occur at depths varying from 1–8 inches and varying between species and soil. Micro-fungi were isolated from "normal" soil and soil in which these fleshy fungi grew. It was found that within the mycelial zone of these agarics the number of species and individuals of micro-fungi was reduced. The cause of this has not yet been adequately demonstrated. In trials with the micro-fungi of the soil, no antibiotic action was demonstrated in agar plates although in the case of 2 of the 3 species especially studied, bacteriostatic substances were demonstrated with standard test bacteria.

The sixth of a series of papers by A. F. Parker-Rhodes (1949–1951) on the Basidiomycetes of Skokholm Island, on the west coast of Pembrokeshire, England, should be the beginning of a new series of reviews rather than the last in an old series, since it introduces an entirely new basis for the concepts which have been used in the study of fungus synecology. This series was initiated with three papers (1949, 1950a, 1950b) on some genetic problems in relation to the autecology of certain agarics found on the island under study and these are followed by a presentation (1951a) of "an elementary theory of anemophilous dissemination" in which only Homobasidiomycetes with violently discharged wind-borne spores are considered and the theory is worked out on a statistical basis. The fifth paper (1951a) is of a taxonomic nature in which a number of

species of agarics are redescribed and a genus introduced.

The paper (1951c) entitled "Some floristic and ecological calculations" presents some very interesting methods of studying problems in constancy of fungi within limited areas. The first striking departure from techniques used previously is the fact that the study is based on mycelia rather than fruit bodies. The position of the mycelium was determined by fruit bodies, i.e., it was determined by aggregation of fruit bodies or arrangement of fruit bodies such as in circles or "fairy-rings."

The area of the island is approximately 240 acres. In collecting the fungi "all parts of the island were perambulated with approximately equal density." This technique was checked by the use of formalized transects formed of relatively straight lines connecting outstanding landmarks along which the observer walked and observed every individual within 126 cm. (¼ rod) of each side of the line. By statistical analysis of data obtained in both ways in 1948 and 1950, it was found that no significant discrepancies were found between the two techniques.

It was found that when more species are observed, the sampling efficiency is increased which may be explained on the basis of a bias: a rich crop stimulates interest and "tends to produce a bias in favour of efficient sampling." It is suggested that this form of bias may be more general than hitherto suspected in ecological work.

The term "locus" is used to describe "a portion of substrate large enough to support one fructifying diploid mycelium, but not so large that two such mycelia could simultaneously fructify upon it." Then the "enumerative habitat" "is made up of all the loci accessible to the species," and their number defines the size of the enumerative habitat. On the basis of Poissonian analyses of data "prevalent" species are determined (the term dominant is not available for use here since it is used for the vascular plants of the area) and the remaining species are considered "subvalent." It was found that prevalents were represented by 3 or more records in any one season, while subvalents were represented by less than 3 records in any one season.

With the use of statistical analyses, Parker-Rhodes was able to determine the total number of species he could possibly have found in September on the basis of the number of species found in each of the 4 Septembers in which the species were studied.

In addition, the influence of the season, habit and habitat on constancy of fructification was studied. Here subvalents were divided into "preposites" which were represented by only one record in any one season, and "apposites," represented by more than one record. Five habit classes were erected on the basis of type of fruit body and at least 10 habitat classes were established based on types of substratum or plant association in which the specimens were found.

Finally, in two appendices, the algebra of the equations used earlier is presented; and a table is given in which 171 categories of fungi are listed alphabetically according to specific and subspecific categories, ecological status (prevalent, preposite, or apposite), habitat, habit, season classes, and distribution.

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THE DRILLING MECHANISM OF THE NATICIDAE[1]

It has never been conclusively determined whether carnivorous prosobranchs of the family Naticidae drill holes through the shells of other molluscs by means of (1) chemical secretions from the salivary glands or similar organs, (2) mechanical rasping with the radula, or (3) a combination of both. The drilling process has not been observed directly because most species refuse to feed above the surface of the sand, and the few that will feed in the open water cover the drilling organs with the foot so that the drilling process is hidden.

A number of investigators have been of the opinion that the hole is made with a flat, disc-like pad that is situated on the ventral surface of the proboscis at the distal extremity. This organ occurs only in this group of prosobranchs, and its size agrees closely with that of the hole. Schiemenz (1891) obtained a reddening of blue litmus paper when touched to fresh pads and concluded that the hole is dissolved with acid secreted by this organ which he named the "boring gland" (*Bohrdruse*).

Hirsh (1915) and Boettger (1930) both held to this view although neither was able to demonstrate the actual secretion of a sufficient amount of free acid to dissolve a hole in the short time in which it is normally accomplished. Later Ankel (1937) placed "boring glands" on glossy shells and demonstrated faint etching of the surface, but was unable to determine the presence of any of the common acids. He finally concluded (1938) that a specific enzyme, "Calcase," might be the active agent.

An opposite view was held by Fischer (1922) who maintained, after histological studies had proved that the pad was mainly a muscular organ, that the hole is bored mechanically with the radula working as a rasp. However, he did suggest that its action might be facilitated by a softening of the calcareous shells with sulphuric acid secreted by the salivary glands. Pelseneer (1925) showed that the salivary secretions contain no acid and concluded that the drilling process is purely mechanical.

The discovery of drilled egg capsules of the marine snail Sipho by Thorson (1935) and of bored egg cases of rays by Jensen (1951) demonstrated that the Naticidae could penetrate noncalcareous substances. Jensen determined that both materials were resistant to sulphuric acid in concentrations as high as two per cent, and also that the edges of the holes were furrowed with minute scratches which he believed were made by the radula teeth.

There appear to be no published records of experiments to determine the ability of the Naticidae to drill through other inert materials. For this reason, two experiments were performed with the American clam drill, *Polynices duplicata*, to test its ability to perforate lamellibranch shells coated with paraffin wax and plaster of Paris. A number of clams (*Mya arenaria*) coated with histological paraffin in layers approximately 0.5 mm thick, were placed

[1] Contribution No. 630 from the Woods Hole Oceanographic Institution.

in a sea-water aquarium containing starved *P. duplicata*. The Polynices readily attacked the coated clams and drilled typical holes without any interference from the wax layers. This established the fact that the drilling process is basically mechanical but did not preclude the auxiliary use of chemical secretions to soften the hard calcareous shell after the wax had been scraped away. A number of clams were then coated with plaster of Paris as a further test. Plaster of Paris is a fine powder which consists of partially dehydrated calcium sulphate. When mixed with an appropriate quantity of water it sets within a few minutes and reaches its full degree of hardness after only a few hours. It is insoluble in dilute acids and organic solvents. The *Polynices* readily attacked clams coated with Plaster of Paris and drilled typical holes through the coatings without apparent difficulty.

The results of these experiments indicate clearly that the Naticidae drill holes through the shells of their prey by mechanical rasping with the radula, unaided by chemical secretions. The function of the so-called "boring gland" is not apparent, but its structure and location suggest that it may be an adhesive pad that holds the anterior extremity of the proboscis firmly against the shell to facilitate the action of the radula.

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A PHYSIOLOGICAL LIGHT TRAP

Color responses discovered in the Cladocera (Smith and Baylor, *in press*) suggest a light trap for their capture. Organisms exposed first to long wave lengths will swim downward upon sudden exposure to short wave lengths.

Although Cladocera are attracted strongly to any weak light, by shining only the long wave lengths (yellow light) out into the water the individuals attracted become properly exposed as they swim in. An arrangement is then made so that, sooner or later after an individual reaches the yellow light, it will swim into short wave lengths (blue light). As it then swims downward it passes through a funnel into a suitable cage.

One version of this principle is shown in Figure 1. It has the advantage of simplicity both in construction and use. The weak light is not a disadvantage; the effect of changing from yellow to blue is greater at low than at high intensities. The colors are controlled by using a Wratten K2 or F filter (Kodak), lining the inside of the test tube from the point "a" upward, and a small piece of blue cellophane in the bottom below this point.

The levels must be adjusted carefully so that no blue light escapes over the top of the funnel. The pen-light bulb is so built that is focuses a sharp cone of light downward, ideal in this case for the blue light.

As organisms swim against the test tube, a downcurrent is set up which is surprisingly efficient in carrying individuals down across the color boundary into blue light. Once across the boundary their own responses do the rest.

This particular trap could be improved in at least two ways: (1) if the blue light were a second source, mounted above the yellow light so as to project a cone of blue downward all around the test tube, organisms would not have to drop first in order to be caught; (2) if the yellow light were polarized so that the plane of vibration were horizontal in the rays shining out, the fishing area would be doubled without increasing the light intensity (Baylor and Smith, *in press*).

Customarily this trap is floated on a lake in the evening and picked up at leisure the following morning. It is specific, not for a taxonomic group, but for a physiological group. If a species is to be caught, it must be attracted to a yellow light and repelled or caused to swim downward upon changing from yellow to blue.

Cladocera caught in several settings include:

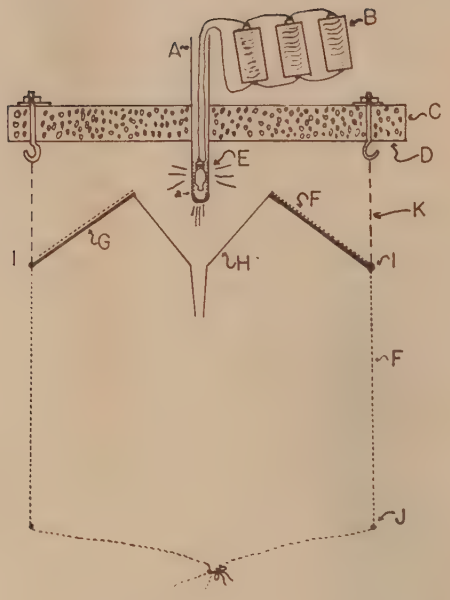

FIG. 1. A physiological light trap for Cladocera and other animals. A, large test tube piercing float; B, three 1.5 volt flashlight batteries in parallel taped around test tube; C, float with four suspension hooks; D, reflecting surface; E, 2.2 volt pen-light bulb; F, bolting cloth; G, six ⅛-inch rod supports; H, ordinary aluminum funnel; I, J, quarter-inch metal rings; K, cylinder of ¼-inch mesh screen as a fish guard hung on hooks.

Sida crystallina (Müller), *Daphnia longispina hyalina* (Leydig), *Simocephalus vetulus* (Müller), *Ceriodaphnia reticulata* (Jurine), *Bosmina obtusirostris* (Sars), *Chydorus globosus* (Baird), *Kurzia latissima* (Kurz), and *Leptodora kindtii* (Focke).

Other organisms caught include the phantom larvae of the genus *Chaoborus*, the swimming larvae of the caddis fly genus *Triaenodes*, and various water mites.

Single catches often numbered hundreds of thousands of specimens.

The collection of carnivorous forms (Leptodora, Chaoborus, and water mites) has its disadvantages. On one occasion, when the contents were removed from the trap at midnight, several hundred Sida and Simocephalus were seen. By morning all save two were gone, eaten by the two hundred water mites that were also taken.

The basic principle of this trap, that of using one kind of light to attract and so condition an organism that a second kind of light will produce a fateful response, should be of widespread application. A trap which samples efficiently a group of organisms with common behavior pattern should be especially useful in ecological studies. Endless combinations of light responses can be used to create a large variety of traps, and by varying their complexity the traps could be made as specific as desired.

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AN INSTRUMENT FOR QUANTITATIVE STUDIES OF PHOTOTAXIS

The phototactic and geotactic responses of Cladocera have recently been investigated by Baylor and Smith and by Smith and Baylor (both papers accepted for publication in American Naturalist). The data reported were qualitative. Quantitative information on the phototactic behavior of Cladocera can be secured with the photoelectric apparatus described below.

While *Daphnia magna* (Straus) was the experimental animal used throughout the present studies, the apparatus should work equally well for other swimming organisms which show positive phototaxis.

The apparatus consists of an aquarium containing Cladocera plus the appropriate photoelectric devices for alternately turning off one light source and turning on another.

The experiments were carried out in a small glass aquarium $8 \times 10 \times 12$ inches. The inside of the aquarium was lined with dull surface black plastic to reduce internal reflections. Two Erb and Gray microscope lamps were arranged to give vertical beams of light through the water to the photoelectric cells beneath the aquarium (Fig. 1). Two one-inch round holes with centers eight inches apart were cut in the black plastic lining of the top and bottom to allow the light to pass through.

Vickers Ltd. barrier-layer cells were used for measuring the population density of animals

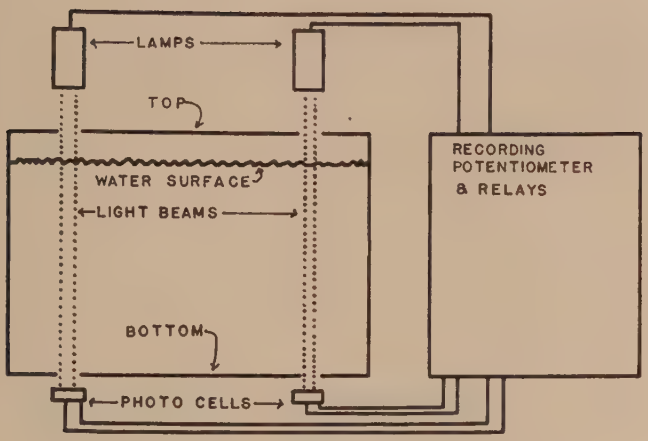

FIG. 1. Apparatus for quantitative studies of phototaxis.

in the light beam (*i.e.*, decrease in light transmission). The signal from each barrier-layer cell was fed to a recording potentiometer such as a Brown Strip Chart Recorder. This instrument is capable of tripping a control relay whenever the intensity of light on the appropriate photocell falls to any predetermined level. The control relay is a ratchet relay which turns on one light and turns off the other simultaneously whenever the relay is pulsed. Since the animals are positively phototactic the result is a shuttling back and forth from one light to the other, the animals changing the lights by their own actions. In addition to controlling the lights the instrument records continuously, drawing each curve of falling light intensity versus time on a moving roll of paper.

No attempt was made to convert the recording potentiometer and barrier-layer cells to a ratio circuit to avoid the uncertainties of line voltage variation. Instead the lights were operated from a Sorensen constant voltage regulator which held the voltage to plus or minus 0.1 per cent.

The phototactic responses to different wavelengths of light were investigated using Corning Glass filters to isolate the desired bands of light. The intensity was controlled with neutral density filters of screen wire of various sizes

The aparatus yields the following information: (1) average velocity of the population (2) the time of arrival in the light beam of any given percentage of the population; (3) distance travelled necessary to kill one-half the population at any given velocity; (4) the effects of wave length and intensity of the light on the above.

Preliminary data for *D. magna* indicate that both intensity and wave length have an appreciable effect on the velocity of locomotion. At a velocity of one foot per minute, 50 per cent of one experimental population was killed in six hours. The surviving members of the population were considerably more transparent at the end of the experiment than at the beginning, due apparently to evacuation of the gut and to use of stored food substances.

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RESURGENT POPULATIONS OF LITTORAL MARINE INVERTEBRATES AND THEIR DEPENDENCE ON OCEAN CURRENTS AND TIDAL CURRENTS[1]

A curious departure from the usual local fluctuations in the populations of marine invertebrates is the sudden appearance of a resurgent population in which the numbers may be hundreds or thousands of times larger than in the immediately preceding or following years. On sandy beaches in several parts of the world are species of bivalve mollusks belonging to the genus *Donax*. Some of these species occasionally experience an enormous increase in the numbers of individuals constituting a local population for one to three years and then re-

[1] Contributions from the Scripps Institution of Oceanography, of the University of California. New series, No. 604.

FIG 1. Small portion of resurgent population of *Donax gouldi* on the beach at La Jolla, California, in the autumn of 1950. This population, with an average density exceeding 20,000 individuals per square meter, extended with some interruptions in a band 2 to 5 meters wide for more than 5 miles along the intertidal zone. Nearly all the individuals are shown in their natural position, with only their posterior ends exposed. One-third natural size.

turn to their former numbers or disappear completely in that locality. The cause or causes which are responsible for their resurgences can seldom be found.

Such local resurgent populations of *Donax gouldi* Dall have been recorded on the coast of southern California at La Jolla in 1894–95, 1909–10, 1913–15, 1931–32, 1934, 1937–38, and have doubtless occurred in earlier years. One of the most extensive resurgences on that coast previous to 1949 was in 1937–1938. At that time the suddenly increased population extended in many locations for several hundred miles along the coast, with the little clams almost in contact and in such vast quantities that they were used extensively for broth and the broth was also canned commercially. In the late summer of 1938 the deaths in this immense population increased to epidemic proportions and by the end of October many of the beaches from Santa Monica, California, to Ensenada, Baja California, were thickly covered with the empty shells. Many of the dying clams were infested with trematode cercariae but although some kind of a minute pathogenic organism was suspected of having been responsible for the deaths, such an organism was not discovered.

The beach near the Scripps Institution of Oceanography at La Jolly was searched at frequent intervals during the ensuing half year but not a single individual could be found in an area where millions had existed a few months previously. The larvae brought in by currents from localities where the extermination had not been complete eventually repopulated the area as small, but fluctuating, populations for the next ten years, although very few individuals grew to more than half the normal adult size.

In the spring of 1949 the local population of *Donax* in the intertidal zone and below did not exceed one individual per square meter but during the summer there came another resurgence, this time of quite unusual magnitude. As the young clams increased in size they were not only in contact but crowded into several layers (Fig. 1). An average of more than 20,000 individuals per square meter formed a broad band from 2 to 5 meters wide in the intertidal zone and extended, with some interruptions, for more than 5 miles along the sandy beaches. This population presumably resulted from swarms of larvae brought by ocean currents from a beach about 11 miles distant or from some other beach within 60 miles, since these currents have an average velocity of 4 to 5 miles per day.

This dense population continued, but with considerable mortality, for almost two years, when approximately half of the individuals died after spawning in July, 1951. Those remaining still formed a dense population in many

areas, but as soon as spawning began the following spring the mortality increased until about the middle of July, 1952, when only about 20 individuals per square meter, or one-tenth of one per cent of the early population, remained. Nearly all of these died within a period of a few days. The deaths included not only the members of the resurgent population, which had then attained the ripe old age of 3 years, but also nearly all the younger individuals which had reached the beach in the two intervening years, and which had managed to survive in the less crowded situations until the final catastrophe. Again, as in 1938, extended search along the beach, both in the intertidal zone and below has failed to reveal a dozen individuals, old or young, with the exception of one small area in which all the members of the resurgent population died, while the younger year-classes survived. Coincident with the final period of mortality was the arrival of a dense population of dinoflagellates but it is uncertain whether these organisms had any influence on the death rate of the clams.

No completely satisfactory explanation for this occurrence has been found. Samples of the population had been examined microscopically once each month or oftener throughout its 3-year history.[2] Infestation with trematode parasites was found in about 10 per cent of the clams and many unicellular organisms thought to be commensal were usually present and the expected minute pathogenic organisms could be detected. The trematodes may render the individual sterile but do not ordinarily kill it. Pelseneer (1928), however, attributed the death of a large population of *Donax vittatus* on the coast of France to heavy infestation with similar cercariae but it seems possible that other minute pathogenic organisms may have been involved.

The life span of *Donax* in this locality is seldom more than 3 years and that may account for the deaths of some of the older individuals but not those of the younger year-classes. The circumstances point strongly to an epidemic disease comparable with one of those that have caused so much mortality among the oysters along the Atlantic and Gulf coasts, as well as in Europe and other parts of the world.

As is usual in this and other species of sand-dwelling clams, the moribund individuals lay fully exposed on the surface of the sand for several days before death, apparently too feeble to bury themselves after having been washed out by the surf. The bodies were thin and watery, often with greenish exudations of blood and blood corpuscles, together with many minute objects thought to be responsible for the epidemic although their precise nature could not be determined.

The reproductive capacity of this species, as of most other pelecypods, is very great, since each mature female may produce 50,000 to 100,000 ova during the spawning season. The fertilized ova develop into pelagic larvae which may be carried for several miles during the larval period by the ocean currents which in this locality, as already mentioned, have an average velocity of 4 to 5 miles per day. Most of the larvae presumably perish because of unfavorable temperature, predation by enemies or adverse currents which carry them too far from shore but others may reach a suitable sandy beach at the precise time when they are ready for transformation to the adult condition.

The inshore currents may flow either north or south and the direction is frequently reversed. For this reason the swarms of larvae may be carried for several miles from their place of origin and when they are ready for settling they may be returned to the beach from which they started. In such a case a continuously maximum population might be maintained. The infrequency of resurgent populations indicates that this seldom happens on this part of the coast, since each beach usually supplies the population for some other beaches.

During the years between the periods of resurgence the species is maintained locally as a small but fluctuating population or it may disappear almost completely. The increase in the population is limited by heavy surf which may carry the clams to far out to sea or bury them too deeply in the shifting sand, as well as by such predators as elasmobranchs, bony fishes and gulls or by trematodes and other parasites. Several species of fishes nip off the siphons but these can be regenerated.

The range of the species is reported to extend from north of Point Conception, California, to the Gulf of California and southward to Acapulco, Mexico, a distance of more than 2,000 miles. At various places along this extent of coastline, it is probable that there are several local resurgences each year, for this is a species that may be very abundant in one locality while it is scarce in another. The differences are presumably caused in large measure by vagaries in the ocean currents which transport the larvae.

There are many examples of similar resurgent populations of marine invertebrates but usually on a less extensive scale. Coe (1946) reported the sudden appearance of a population of the bay mussel (*Mytilus edulis diegensis* Coe) on the coast of southern California. In 1943 a small colony of this subspecies was found on the pier at La Jolla where none had been seen in the immediately preceding years. The following summer the mussels had multiplied

[2] The writer is indebted to Mr. James Kittridge of this Institution for assistance in making some of the collections.

so rapidly that they covered all the available spaces in the intertidal zone on the pier as well as on most of the adjacent rocks. In many situations there were a hundred times as many young as could have grown to maturity because of lack of space. Vast colonies were started in places unsuitable for survival.

They were soon distributed widely along the coast and in some localities became a nuisance by attaching themselves to boats and piers, as well as by clogging the intake pipes of salt-water cooling systems. Following that resurgence the numbers decreased to relatively small local populations. The larvae may be carried for many miles by the ocean currents during their pelagic existence.

The wide fluctuations in the populations of the Pismo clam (*Tivela stultorum* Mawe) at Pismo Beach, California, from 1927 to 1949, are tabulated by Coe and Fitch (1950) from the annual census made by the California Bureau of Marine Fisheries. The relative size of the population each year was estimated by collecting all the clams on a definite area of the beach. Although there were millions of clams on this and adjacent beaches and each large female can be expected to produce more than 10,000,000 eggs each year, the number of young which became established on the beach was relatively extremely small. This number has been highly variable, however, presumably because of the fluctuations in the environmental conditions, including the vagaries of the ocean currents which must be depended upon to bring the larvae to the beach at the end of their pelagic stage.

In the measured area there were only 6 yearling clams in 1928, as compared with 468 the following year. None were found in 1934 but there were 758 in 1935; 743 in 1937 and only 9 in 1938, and 1 in 1949; in 1950 and 1951 there were none. No evidence has been found of any change in the spawning activities of the clams, nor has there been any considerable variation in the environmental conditions. It is therefore concluded that adverse ocean currents have carried the vast swarms of larvae too far out to sea or to some other areas along the coast, many of which are not suitable for the survival of this species. The small numbers in recent years are not considered as evidence that more favorable conditions with a resurgent population may not appear in the immediate future as the result of random fluctuations in the environment, including the direction of the ocean currents.

The great variability in the number of yearlings in the measured area in successive years is shown by the following list, beginning with 1927: 37, 6, 468, 357, 871, 44, 199, 0, 758, 142, 743, 9, 23, 24, 13, no record for 1942 to 1945, 384, 31, –, 1, 0, 0. For the first 12 years there is indication of a biennial periodicity, each alternate year, beginning with the first, having a larger population of young than each intervening year. No satisfactory explanation for these observed fluctuations has been found. The environmental conditions are not known to have shown corresponding variations, but it may be suggested that one of the reasons may have been that adverse ocean currents in the years with the smaller populations carried most of the larvae away from the beach when they were ready for settling. Otherwise the series shows no evidence of a cyclical periodicity.

Records of the set of young oysters in Long Island sound for the past 70 years, compiled by Loosanoff and Engel (1940) likewise show very wide fluctuations in numbers. Heavy sets were reported in 12 of the 18 years prior to 1900 but there have been only 6 years since that date when the sets were considered heavy. From 1906 to 1924 there were only light sets and failures, with medium sets in 1926, 1934, 1937, 1941, and 1945. Heavy sets occurred in 1904, 1925, 1928, 1930, 1939, and 1940. These records likewise show no evidence of a cyclical periodicity.

Not only the larvae of the species mentioned, but also those of other littoral invertebrates such as most bivalve and some univalve mollusks, worms, crustaceans, echinoderms, tunicates and others which have a prolonged pelagic existence may be carried several to many miles from their place of origin. Their survival depends not alone on the vicissitudes encountered on their journey but also on the chance of arriving at some suitable locality at the time when they are ready for metamorphosis and settling on or in the substratum.

They may then repopulate a depleted area or complete with the resident population for food and space for attachment or shelter. Furthermore they may maintain a population in localities where reproduction does not usually take place. The chances of reaching a place suitable for existence as adults are obviously greater in bays and partially enclosed bodies of water than on the open seacoast where so many of them are likely to perish by being carried too far out to sea.

During certain tidal periods in bays, sounds and estuaries the larvae may be carried back and forth at rates of several miles an hour. Many of them are drifted too far out to sea or to other areas which are unsuitable for survival. Likewise larvae from the open coast may be brought into estuaries where the salinity is too low or where other conditions are unfavorable.

By means of these currents the geographical range of a species with pelagic larvae may be extended in favorable seasons far beyond the usual limits but only to have the range restricted again when more rigorous conditions

return. The population will thereby fluctuate irregularly in distribution and in numbers, with an occasional resurgence in varying degrees of magnitude.

It is concluded that resurgent populations of marine littoral invertebrates in any locality depend upon a combination of the following circumstances: (a) a large spawning population at that locality or at some other place not too many miles distant; (b) suitable conditions during the period of pelagic larval life; (c) favorable currents which may bring the swarms of larvae to that locality at the exact time when they are ready for metamorphosis to the adult form and settling in or on the substratum; and (d) adequate opportunities for continued growth.

As a consequence of these currents, local conservation measures usually have little influence on the subsequent populations of that immediate neighborhood, although they may benefit some other locality to which the larvae may be carried. In order to be effective in any one locality it is therefore necessary that the conservation should include a sufficiently large extent of coast line to insure that each locality may supply larvae to the others. Only occasionally will a large proportion of the larvae be returned to their place of origin.

Summary

Resurgent populations of the bean clam, *Donax gouldi*, have occurred on the beach at La Jolla, California, seven times during the past 58 years. On most of these occasions the local population was a thousand to ten thousand fold larger than in the immediately preceding or the following years. These populations doubtless resulted from the arrival of swarms of pelagic larvae which originated elsewhere and were brough to the local beach by ocean currents at the time when they were ready for transformation and settling in the sand.

Such populations of *Donax* are always short lived. In one of them, numbering 20,000 individuals per square meter one year after arrival and extending in a band 2 to 5 meters wide for 5 miles, disease was prevalent, mortality rate was high and, with very few exceptions, all the members of this immense population were dead within 3 years.

Less extensive resurgent populations are reported for the Pismo clam, the bay-mussel and oysters. The local abundance or scarcity of other species of marine littoral invertebrates with pelagic larvae, including those of economic importance, likewise depends to a large extent on the vagaries of the ocean currents or tidal currents which may bring the larvae to that locality at the time when they are ready for transformation to the adult condition and settling on the substratum.

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RECESSION OF EELGRASS AT CAPE ANN, MASSACHUSETTS

The late Neil E. Stevens, well known phytopathologist, remarked on many occasions that the disappearance of eelgrass (*Zostera marina* L.) from the Atlantic coastline as the result of a wasting disease, was the greatest biological phenomenon that he had ever observed. A posthumous paper organized by him (Stevens, Ellis, and Stevens 1950) summarized the subject of eelgrass wasting and recovery on the Atlantic coast of the United States. J. G. Mackin has recently reviewed the literature in a privately circulated processed report.

The writer has observed the eelgrass situation at Cape Ann, Massachusetts, at various intervals over the past 19 years. A brief report (Dexter 1950) described the reëstablishment of the Zostera faciation in 1949 in a single cove (Goose Cove) at Annisquam on Cape Ann. For nearly three years this eelgrass community continued to exist with a solid stand of healthy eelgrass throughout the cove (Dexter 1951). Notes have also been given in former reports on small, scattered patches located elsewhere in the Cape Ann region.

In middle September, 1952, a return visit was made to the area. Observations made at that time are reported here. At Wingaersheek Beach on the shore of Annisquam Harbor,

FIG. 1. View of Goose Cove at low tide in August, 1951. The eelgrass community is shown at the peak of its reëstablishment eight months before its total destruction.

small scattered clumps and individual plants of eelgrass persisted in a narrow zone along the spring-low-water line. No change since the previous year was evident. A survey through most of the Annisquam River (tidal inlet) failed to disclose any growth of eelgrass. This survey was not as thorough as the one of the preceding year since the latter was conducted during a minus tide. The four patches of eelgrass discovered in 1951 were not seen in 1952. However, evidence from the survey and from reports contributed by clammers, lobstermen, and those boating and swimming in the river indicated that no perceptible change had taken place. The same conclusion was reached regarding eelgrass growth on the ocean shores of Cape Ann.

At Goose Cove, on the other hand, the eelgrass community which had slowly recovered from the wasting disease over a period of about 8 years was completely destroyed. Figure 1 shows the eelgrass community at its height in August, 1951. On April 11, 1952, two earth dams, one on each side of the causeway, closed off inner Goose Cove while the bridge over the sluiceway was rebuilt. The dam was closed at low tide. Some salt water leaked through the dam and fresh water from the drainage of a small brook and domestic sewage soon filled the cove. In the absence of tidal currents the accumulated fresh water and pollution killed out the eelgrass and most of its associated animal life. The dam was removed on August 21. Survivals of marine life included a few of the English periwinkles (*Littorina littorea*), and some of the blue mussels (*Mytilus edulis*). At the marsh level survival was high among the ribbed mussels (*Brachydontes demissus*) and the marsh grasses (*Spartina alterniflora* and *S. patens*) seemed to be little affected since they were above the level of stagnant water for the most part. A small amount of rock algae (*Ascophyllum nodosum* and *Fucus vesiculosus*) persisted on the rocky shores. The rock barnacle (*Balanus balanoides*), the most common species of barnacle at Cape Ann, apparently did not survive in the cove while the ivory barnacle (*B. eburneus*), an uncommon species in the area, had a surprisingly good set in the brackish water which soon filled the cove. Because the water level remained high the ivory barnacle replaced the rock barnacle on what is normally the intertidal zone within Goose Cove. Continued stagnation, however, did not permit a high degree of survival (less than 50 per cent), and since tidal fluctuations have been restored this species, partial to brackish water and continuous submergence, will probably not persist here long.

Eelgrass patches which had developed in outer Goose Cove during the past 7 years were not present in September, 1952. Possibly they were destroyed when the polluted water impounded in the cove was released upon removal of the temporary dams. On the other hand the eelgrass may have failed through natural causes.

George Gleason reported that a patch of eelgrass observed in 1951 at the mouth of Essex River on the northwestern edge of Cape Ann was not found in 1952.

As a result of elimination of eelgrass in Goose Cove and the failure of the plant to become reëstablished elsewhere in the area, this species and Zostera faciation have once again disappeared as ecologically important units at Cape Ann. Whether they will return to Goose Cove only future observations will tell; their return to the Cape Ann region have been seriously jeopardized by the destruction of the only extensive and healthy stand of eelgrass which has developed in this area since the epidemic of 1931–33. Acknowledgment is made to Ralph Hendrickson, Harold Geary, George Gleason, Herbert Montgomery, and Charles Heberle for assistance in this study.

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REVIEWS

Rainforest, Savana and High Mountain in Bolivia [1]

The vegetation of South America has been mapped on small scales many times (Drude, Engler, Schimper, Denis, Rübel, etc.). Although these various representations do not completely coincide, they have left with us a fairly coherent picture of the continent's plant cover. We have, on the other hand, a more intimate knowledge of some small or local areas for which data of a quantitative nature are available. Guillermo Mann now offers us a general view of plant and animal life in Bolivia. The maps are in no way an improvement over preceding ones, some of which are indeed a good deal more precise in their outlines (but maybe unjustifiably so). Nor can it be claimed that any description of plant community adds considerably to our previous knowledge of it. The merits of this book lie elsewhere.

In the first place the contents do conform to the title, which is not always so of books that advertise themselves as "ecological." An authentically ecological point of view prevails throughout. Moreover, the author shows an awareness of the shifts of emphasis that have taken place in biological thinking since Warming and Schimper's time, as he also makes us aware of the many challenges made by these early vegetationists which have been forgotten by more recent investigators.

The book consists of three parts: I selva, II savana, III high mountain. The analysis is a very symmetrical and logical one which makes excellent reading and offers easy cross-reference. In each part the first chapter concerns spatial extension; the second describes physiognomy, life-cycles, adaptive features, and ecological factors; the third outlines variations within the formation (especially in ecotonal areas) and successional dynamics.

The very symmetry of such treatment results in chapters of somewhat uneven value and an approach which is sometimes a little abstract. However, the numerous examples of plants and animals actually observed and photographed by the author and sketched in drawings by Serena Mann de Pfeil give each chapter the substance and the reality which it would otherwise lack. In his preface, Mann states that his object is to convey "a first glance of the prevailing harmonies" of the Bolivian environment and of its "larger biotic units." His book he considers an "ecological guide." Its usefulness is extended to a non-Spanish-reading audience by the interpolation of an English and a German summary, which are quite substantial. However, the latter contain only the theoretical conclusions and the reader will still have to refer to the Spanish text for a citation of examples and a concrete description of organisms and phenomena. The English wording and syntax are not always perfect and the spelling is frequently in error, but only rarely do these faults actually disguise the author's meaning (amphibiotic for amphibious).

It would hardly be fair to say that this sweeping review of a relatively large segment of the tropical world is superficial, as it could hardly be otherwise unless the book were five times its present length. Rather it remains to evaluate the accuracy and consistency of the concepts applied and to judge the sharpness of the picture which is conveyed.

Clements and Shelford's terminology and method are adhered to, and some of their keywords are re-defined. However, to this are added so many physiognomic-structural and autecological observations (in the tradition of Warming, Schimper and Hesse) that the "bio-ecological" framework does not actually prevail. An attempt is made, for instance, to recognize *biomes*, but is hardly followed through. In fact, it is clear that three *formations* are being studied, and within them only the broadest ecological units are recognized and then are tagged with ordinary vernacular names, such as "flooded savana," "forest pools," etc. The life-form, structure and abundance of dominants is very clearly described in each case. The author repeatedly mentions their influence on climate, whereas he evidently means microclimate (the evolution of meteorological elements within the community). However, the physiognomic picture is always completed by a description of the adaptations which are most typical of the formation or community, irrespective of the spatial importance of the organisms in question.

Although he seems to accept wholeheartedly the monoclimax theory and cites many successional sequences in both xerosere and hydrosere, the author shows awareness of the many factors that retard and inhibit succession and describes many edaphically-controlled communities.

The brief bibliography at the end of the book is hardly cited in the text. One feels that the author is familiar with many other works not mentioned here and he would have in-

[1] **Mann F., Guillermo.** 1951. Esquema ecologico de selva, sabana y cordillera en Bolivia. 236 pp. Universidad de Chile, Facultad de Filosofia, Instituto de Geografia, Publ. No. 3.

creased the usefulness of his book by listing them for reference and citing them in the proper place in the text.

As it stands, the book is certain to offer much stimulation to further research and exploration. The descriptions will be developed by local study and the principles and laws will be tested by comparison, discussion and new investigations.

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INTEGRATION OF THE ECOSPECIES [1]

The eternally disputed definition of species is very sharply focused in Jens Clausen's book, "Stages in the evolution of plant species." The outstanding merit of this work is that it summarizes very lucidly the experiments on the nature of species which Hall had begun but which are principally Clausen's own work and that of his collaborators David D. Keck and Wm. M. Hiesey at the Carnegie Institution of Washington's Department of Plant Biology in Stanford, California. The past decade has been a very fruitful one for this group, as the essentials and much of the detail of their experimental work have been made known in print. The soundness of their method, the thoroughness of their investigations and the variety of their respective backgrounds offered unique guarantees of original and significant research. Their three book-length memoirs and their many shorter papers had provided us with a great wealth of new materials and many leads to new interpretations. The present book goes a step beyond this and outlines Clausen's (and presumably his collaborators') emergent concept of speciation. This is far-reaching indeed, although the author does not pretend to review the whole field of experimental taxonomy, even less the more general topic of evolution. In fact, it justifies its title perfectly by casting complete emphasis on experimentally known cases of perfect to imperfect to inadequate isolation of taxa in the Western North American environment. Some of the author's earlier work in Northwestern Europe is also quoted, as are Brainerd and Gershoy's in Eastern North America. But no one will quarrel with Clausen's dwelling principally on what he knows best: a central Californian transect from the Pacific across the coastal ranges and inner valleys to the slopes and summits of the Sierra Nevada, thence down to the deserts of the Great Basin. Such a transect lends itself extremely well to a test of evolutionary processes as it provides strongly contrasting environmental backgrounds at close intervals. Even though such telescoping is not unique, it is in many ways peculiar and the rates of change and the very mechanisms observed are sure to be quite different in other parts of the world with broad instead of narrow life zones. Stebbins for instance (Am. Nat., **86** (826) : 34, 1952) ventures to "predict that the diversity of ecotypes of individual species, when investigated will prove to be considerably less" in the Eastern States than in California.

The book consists of eight chapters. The first two offer a brief historical perspective in which the growing influence of genetics on taxonomy is emphasized. The principal currents are outlined: Darwin's keen observations of variation in nature and its obedience to natural selection; the experimental approach and discovery of the mechanics of heredity by Mendel's successors. These two traditions, which to some extent had followed separate courses, are joined harmoniously in Turesson's work. The often overlooked evolutionary ideas of Linnaeus in his later years are quoted as marking the beginning of a "modern" point of view. Jordan is credited with the discovery of the local population.

This is the subject of the third chapter, "The local population as the basic evolutionary unit." Here the author's working principles are clearly stated: "It is at the level of the local population that all of the selective forces act upon the genetic resources of the population." This statement is well illustrated and substantiated by examples from the genera *Layia, Viola, Potentilla,* and *Achillea.* Following the best in taxonomic tradition, intra-population and inter-population variations are compared and found to be of a different order of magnitude (p. 26). However, these analyses are always made in the light of the deeper-lying physiological responses which are elicited by the heredity *vs.* environment contest. Thus: "It is probable that the intrapopulation variation enables a species to tolerate periodic variations in the climate at any one locality."

These various points are strikingly illustrated by experimental data, the conclusiveness of which is quite incontestable. One might wish, however, that Clausen's rejection of other techniques for estimating populations "growing in the wild and therefore subjected to uncontrolled modifications in many environments" were the object of further discussion. The work of Edgar Anderson, Fassett, and Woodson is not men-

[1] **Clausen, Jens.** 1951. Stages in the evolution of plant species. viii + 206 pp., 76 figs., Ithaca: Cornell University Press, $3.75.

tioned. It would be interesting to compare purpose and achievement in both cases and to outline what aspects of environmental integration are revealed by these different means. It seems, however, that both groups will agree that "clines are not commensurable with natural entities," if by the latter are meant formal taxa.

The fourth chapter concerns "the evolution of ecological races." Whereas the preceding chapter had not provided a hard and fast definition of the local population, the present definition of the ecological race may seem unsatisfactory: "An ecological race is usually composed of a considerable number of variable local populations existing within a given ecological zone." This latter term itself is not defined either, except by implication. A short paragraph on parts of pp. 50–52 states that "these major sets of factors in the environment have been decisive in the development of ecological races, namely, climate, soils, and other organisms. All of these three are interrelated and contribute to natural selection, but climatic, edaphic, or biotic ecotypes can be recognized, depending upon which of these sets of factors has been relatively the most dominant."

I can voice no objection to the above statements but I am afraid they lend themselves to a variety of rather divergent applications. Whereas a constant attempt is being made to assess morphological, genetic, cytological and physiological criteria and to assemble them in a discriminating way so as to reflect a natural hierarchy (Chapter VIII), and whereas the magnitude of each "stage in the evolution of plant species" is graded, no corresponding hierarchy in the environment as a whole is indicated. Transgressions by the segments of a species beyond the barriers of biotope, community, habitat, climatic zone are not recognized explicitly as such.

Clausen does not say that hierarchy in environment (*a*) does not exist; (*b*) is too complex to be measured effectively; (*c*) is not significant, since the ultimate unit alone is considered. For instance, Figure 5 (p. 20) shows 4 subspecies of *Potentilla glandulosa* as they occur from 900 to 11,000 feet on the west slope of the Sierra Nevada. As far as major climatic and vegetation zones are concerned, 6 distinct units are involved: 1) the oak savana, 2) the yellow pine forest (or woodland), 3) the red fir forest, 4) the lodgepole pine woodland, 5) the white-bark pine scrub and 6) the alpine meadow. Ssp. *typica* is found only in 1; ssp. *reflexa* in 1 and 2; ssp. *hanseni* in 2 and 3; ssp. *nevadensis* in 4, 5, and 6. The case of *reflexa* and *hanseni* is an interesting one as they overlap to a considerable extent geographically (and therefore climatically), but remain distinct ecologically. Thus some local populations of both subspecies share the same amounts of rainfall and heat except inasmuch as their habitats ("sunny slope" and "meadow") utilize the meteorological elements differently and eventually provide the plants themselves with rather different amounts of heat and water, and at different times also. There is here an ecological dimension that fits into a climatic dimension. There is also the further question of ecological amplitude, not necessarily similar or even parallel to climatic tolerance.[2] Although these issues are certainly present in the author's mind, they are not as sharply focused as the corresponding morphological and genetic aspects.

In the fifth chapter the genetic systems which underlie the adjustment of taxa are reviewed, whether or not the units involved show any morphological discreteness. The point is well made that some formerly adaptive features are able to persist after a shift and even a reversal in the kind of environmental pressure exerted. Thus a "typically maritime" *Viola tricolor* (from Denmark) was grown in inland California and eventually sowed itself in a garden at Santa Rosa, maintaining its identity under "drastic changes."[3]

Several good examples are provided here that illustrate the degrees of effectiveness in genetic isolation. It is assumed that the best proof thereof lies in the failure to cross-breed or in the relative weakness of the offspring. Thus the background is drawn for the principal argument of the book which will culminate in a grading (Chapter VIII) of the isolating mechanisms. The largest stock of evidence along these lines is drawn from taxa indigenous to at least one of the three stations (Stanford, Mather, Timberline) operated by Clausen and his collaborators. The relative frequency of successful experimental crossing on the one hand, and the degree of survival and "vigour"

[2] A plant like *Chamaedaphne calyculata* ranges from the near-Arctic to the mountains of Georgia, is exposed to a variety of severe and mild climates. Ecologically it is very narrow, however, being strictly confined to bogs, and even to a certain phase of bog formation. On the contrary, *Betula populifolia* has rather a narrow range (Atlantic-North Appalachian) but very wide ecological amplitude: sand plains, bogs, old fields, stream edges, rock outcrops, etc.

[3] A similar case is that of *Veronica peregrina* var. *laurentiana*, an estuarine ecospecies now self-sown in the Montreal Botanical Garden where it maintains its identity perfectly. (M. Raymond and J. Kucyniak in Contrib. Inst. Bot. Univ. Montréal, 62: 19. 1947).

in each one of the three stations on the other hand, show both the amount of divergence between related taxa and the amount of relative fitness of each to its station, although not as obviously to its habitat(s), even less to its community(ies).

Chapter VI outlines "the evolution of interspecific barriers," starting with a "situation within species where such barriers have not yet started to evolve," or at least where they are not effective because of gene flow through intermediate segments.

Although "there are numerous ways in which groups of populations and races may become genetically isolated . . . the most normal pattern of speciation . . . is a more or less simultaneous and gradual separation in morphologic, ecologic, genetic, and cytologic characteristics." Clausen then goes on to review "groups having predominantly ecological barriers," "predominantly morphological differentiation," "predominantly genetic barriers." These three different kinds of taxa are amply illustrated by Californian examples, each type showing well-defined characteristics both in morphology and behaviour.

As weak barriers tend to become strong, so scarcely separable units separate further, and better individualized taxonomic units result. In Chapter VII, the author applies the foregoing principles and further synthesizes the wealth of facts at his command to describe "the evolution of groups of species." The genera *Layia, Madia,* and *Hemizonia* in California show very distinct patterns which are essentially the result of different degrees of divergence at all levels, from the local population to the genus. The violets, on the other hand, offer a more complex situation, a greater variety of evolutionary patterns, which is only in part due to their wide geographical distribution.

The last chapter, entitled "The physiologic-genetic species concept and the dynamics of the evolution of species and genera" offers a concise but extremely lucid review of the sources of genetic variability and the means by which it is produced. The excellent Figure 72 shows at a glance the "building blocks" of heredity (genes, chromosome segments, chromosomes, genomes), the process by which they operate (creative mutation, recombination, loss, duplication, addition); and the evolutionary level on which they function (intra- or inter-specific). Two further tables (74 and 75) offer a key to a rational taxonomic hierarchy of categories based on the principles previously outlined and tested. This codification of the dynamic aspects of speciation which has now been forced to the attention of even the most conservative systematists will be most welcome. It seems that *comparia, cenospecies, ecospecies* are necessary terms at this time, although taxonomists are justly reluctant to speak in terms of "morphological species" and "genetic species" (terms which are generally avoided in this book. Rather they are willing to test this and that taxon by the use of new criteria (genetic, ecological, and otherwise) and to redefine and recast them nearer to experimentally known reality without deviating from the classic nomenclature. This however is essentially a "legal" point of obviously little biological interest. It remains that the experimental taxonomist, when he deals in ecospecies, cenospecies, etc., has a more unequivocal term than the taxonomist whose categories are for the most part untested.

Clausen's book is an exceedingly important one to ecologists. If their research is concerned with autecological relationships, they can make no beginning unless they constantly bear in mind the phenomena which are so capably outlined here, unless they are at all times aware of the underlying mechanisms of variability in local populations and ecological races and become able to detect them. Although this little book does not cover all phases of the integration of plants in their environment—which is indeed not its purpose—it so sharply focuses the genetic substratum of adaptation that it provides a useful background for practically all cases.

If the ecologist's research concerns synecology, he will find much that is lacking in this book. He will regret that synecological concepts are nowhere as clear as are genetic and taxonomic concepts. He may feel that much has been said concerning the inherent mechanisms of hereditary transmission, their emergent result as moulders of minor or major taxa; that much has been made also of natural selection as a controlling force. But he will find that it is not too clear *what* the taxa which are used as examples have become or are becoming adapted *to!* He will also honestly have to admit that ecologists, as yet, have hardly provided workers in other fields with a satisfactory repertorium of units as manageable as the species of the taxonomist or the genome of the geneticist. This task lies ahead; now that ecospecies and ecotypes are beginning to be known, it will be worth while to project them against the smallest environmental units that contain them and to evaluate natural selection in terms of the kind, quantity, and durability of pressures that govern *their* dynamics.

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Three Kings Islands of New Zealand [1]

Native organisms, both plant and animal, have always been in competition for space and food, but today there is a new overwhelming force. One competing organism, man, has reached the point where, to meet his own needs and desires, he can direct forces to deliberately eliminate large segments of the fauna and flora. Sometimes a race, as such, is destroyed biologically, as, for example, when the federal government placed domestic reindeer on Alaska Peninsula, where Grant's caribou was struggling for survival. *Rangifer a. granti* is undoubtedly submerged, and no longer exists as such.

In 1949, I had opportunity to visit some areas in New Zealand where native organisms were struggling to recover from depletion, under complete protection. Such a nature reserve is Kapiti Island. On the other hand, the Waipoua Forest, containing some of the last Kauri pines in New Zealand, is an unspoiled remnant which the people are endeavoring to keep intact. I was also told about the Three Kings Islands, off the northern tip of New Zealand, which have a special appeal for New Zealand scientists.

Two issues of the Records of the Auckland Institute and Museum are devoted to the Three Kings Islands. The Islands were discovered by Tasman in 1643, at which time they were inhabited by Maoris. Those early people had already greatly modified the vegetation by their agriculture, and after the Maoris left, over a century ago, feral goats proceeded to complete the disastrous alteration and depletion of the flora. However, in 1946 the New Zealand Government sent expert hunters to the islands, who succeeded in exterminating the goats.

Fortunately, early observations on the vegetation are on record. Quadrats have now been established and much information is being recorded on the surprising recovery of vegetation since the goats left. Dr. Gilbert Archey, Director of the Auckland Institute and Museum, in a foreword, says that the plan is to make frequent visits to the islands "whereby the present studies will be followed by detailed descriptions of the progress of regeneration and of the phases through which it may pass."

The two numbers of the "Records," as noted above, contain a great variety of papers: A chronology of exploration of the islands; general accounts of "The Flora of the Three Kings Islands" by Dr. W. R. B. Oliver; a discussion of "Incipient Forest Regeneration on Great Island, Three Kings Group" by G. T. S. Baylis; and others on the effects of goats on the islands. E. G. Turbott records the birds, and there are notes on the geology. Dr. Archey reports on Maori carvings. In the course of the studies, there were found a new species and subfamily of Opiliones described by R. R. Forster; three new species of land mollusca and discussion of mollusc occurrence, by A. W. B. Powell; a new monotypic genus of the Myrsinaceae, *Elingamita,* by G. T. S. Baylis; "Collembola from the Three Kings Islands with a description of *Proisotomina,* New Genus," and new species and records of Orthoptera and Lepidoptera by Dr. J. T. Salmon; and a new *Anthornis* by Dr. R. A. Falla. The occurrence of the genus *Hoplodactylus* in New Zealand is treated by N. G. Stephenson and *Succinea archeyi* by H. E. Quick.

Turbott presents interesting observations on how the feeding habits of the red-billed gull, *Larus novaehollandiae,* have been instrumental in the establishment of the puka, *Meryta sinclairii,* on Great Island, from the mainland, after the removal of the goats.

These papers demonstrate that birds and vegetation are now recovering, and that there are endemic island forms in both the fauna and flora. We in America are striving to save primitive areas *before* their destruction. Here we have an interesting and significant example of natural recovery *after* depletion.

Dr. Archey informs me that plans are under way to organize a New Zealand Ecological Society. Nothing could be more appropriate in a land where conflicting biological elements have been struggling for equilibrium, and where practical biological problems so urgently need the application of ecological method. The New Zealand scientists are to be congratulated, and we would do well to keep our eyes on the events in that fascinating country.

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[1] **Archey, Gilbert** (ed.). 1948, 1951. Report of the Three Kings Islands expedition. Records Auckland Inst. and Mus. **3** (4, 5), £1, and **4** (2), 10/-, Auckland.

Field Crop Insects [1]

In this text designed for students of agriculture, Professor F. A. Fenton has presented "essentially the subject matter" (p. vii) of a course on field crop insects given by himself over a period of years at Oklahoma A. & M. College.

The division of the text is into two parts. The first of these, covering a little less than half of the book, is intended to provide the student with "a thorough understanding of the basic principles underlying the protection of crops from insect attack" (p. vii). In this section are covered the abundance and distribution, biology, and control of insects. The second part deals with specific insect problems of field crops, grouping them by method of attack and plant parts injured. A brief discussion of the biology and a summary of recommended control measures are given for the individual pests. Each chapter is followed by a series of references. These are not as extensive as might be desired but do direct the student to more detailed reading.

In a field as rapidly changing as that of agricultural pesticides, a book of this type can easily be criticized. The control measures for some of the pests are of questionable value and others have already been outdated by newer materials. The book is not intended as a reference book for the economic entomologist and the control methods sumarized are of historical interest when not of practical value. The diversity of control measures mentioned, and the emphasis on those other than chemical should prove suggestive to the agricultural student.

Although it is desirable that a text of this type should not be overburdened by physiological, morphological, or taxonomic detail, it is difficult to accept a book on insects without an indication of what is considered an insect and how insects are classified.

The section on the biology of insects (pp. 43–53) seems much too brief to provide background for the thorough understanding desired by Professor Fenton. For example, it is improbable that the student will accept parthenogenesis as "the simplest form of insect development" (p. 225) with so little text discussion of insect reproduction (pp. 16–18, 43).

This book should be favorably received by the undergraduate student of agriculture. The information contained is well presented and knowledge gained from the text should aid the student in better understanding the role of insects and their control in field crops. The developing complexity of farm operations today makes this imperative; Professor Fenton has contributed to this need.

The paper is of good quality and the text is for the most part excellently illustrated.

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[1] **Fenton, Frederick A.** 1952. Field crop insects. ix + 405 pp., 224 figs., 10 tables. New York: The Macmillan Company, $5.75.

Forest Entomology [1]

A timber crop requires many years to mature at best, and although forest trees can take a small amount of punishment from insect pests without being appreciably damaged, their economic protection from seed to crop demands careful planning and action based on knowledge of the ecological factors involved in the production of the quantity and quality of the wood desired. This holds whether the control methods are carried out by silvicultural management of the stands or by the application of insecticides and is emphasized by the necessity for proper reproduction in our forested areas and the many uses to which wood is being put. Ever since the first edition of this book was published (1929) Graham has held to this ecological viewpoint and has organized the text according to the habitat of forest insects and the manner in which they injure trees and wood products.

One of the important steps to be taken in any insect control operation is the detection of injurious pests and the determination of their population density in relation to injuriousness, in other words, a survey of insect injury and numbers. The author has introduced in this last edition a chapter on this subject.

The section dealing with insecticides is by no means the strongest in the book, but the proper use of these materials is summarized. The low cost and general efficiency of insecticide application with airplanes has resulted in recent years in extensive use of these machines, and there is a discussion of the use of aircraft for spraying and dusting purposes. "Chemical" control, however, as the author emphasizes, is an emergency measure at best in the forest and may involve undesirable after-effects. The re-

[1] **Graham, Samuel Alexander.** 1952. Forest entomology. 351 pp. New York: McGraw-Hill Book Co., $6.00.

sults of the proper use of insecticides, nevertheless, are usually clear cut and more definite and easily assessed than results attained through stand management.

This third edition represents a rather complete revision. The text material has been reshuffled, the phraseology has been changed, additions have been made, and some parts have been cut. Much of this change is an adjustment to information acquired during the last ten years. The size of the book, however, is about the same, although the number of illustrations is much less than the 1939 edition contained. The author has made a definite effort to keep the size of this volume within what he considers reasonable limits, but there are places where an expansion of data would be beneficial.

During the last 12 years entomologists have gone off on an insecticidal "binge," and it is a relief and pleasure to read an entomology text book in which the information, while bearing on pest control, is predominately ecological.

The dedication is to F. C. Craighead, former chief of the Forest Insect Division, Bureau of Entomology and Plant Quarantine, for whom Graham, in company with other forest entomologists in the United States, holds the highest esteem.

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Carbon Dioxide Fixation and Photosynthesis [1]

There was a time, not long ago, when the study of carbon dioxide fixation was the exclusive concern of plant physiologists. The first break in this monopoly came in 1935 when Wood and Werkman discovered carbon-dioxide fixation in heterotrophic bacteria. This finding brought the microbiologist most actively into investigations of CO_2 metabolism. Then, about 1940, three independent groups of animal biochemists, working in Sheffield, Chicago, and Ames made the almost simultaneous discovery that animal tissues could fix labelled carbon dioxide in the form of dicarboxylic acids. Since then, plant physiologists have taken a back seat in the exciting attempts to chart the path of carbon subsequent to its initial fixation.

This volume, the fifth in the post-war series of excellent Symposia produced by the Society for Experimental Biology, is the outgrowth of a conference on CO_2 fixation held in Sheffield in July, 1950. It is an important addition to the growing literature of comparative biochemistry. The reader gets a distinct impression of the fundamental similarity of mechanism of CO_2 fixations in very diverse creatures. The photosynthetic organisms have certain unique reactions for accomplishing the reduction of fixed CO_2, but by and large, the green cell, the heterotrophic microorganism and the pigeon liver slice appear to respond in similar ways to an external supply of CO_2. In these days of growing complexity of biochemical pathways, such apparent unity in the world of nature is comforting.

The book opens with a chapter by H. A. Krebs on the general historical background, extent and significance of CO_2 fixation in animal tissues. H. G. Wood follows with a summary of the major biochemical reactions involved in the actual fixation, giving especial emphasis to the formation of oxalacetate from pyruvate by the β-carboxylase, and to the formation of malate from pyruvate by reductive carboxylation involving the participation of reduced TPN. S. Ochoa then discusses the biosynthesis of di- and tricarboxylic acids by CO_2 fixation, again placing emphasis on TPN- linked enzymes such as the malic enzyme. Ochoa introduces the first link with the problems of photosynthesis in his announcement of the finding of Vishniac and Ochoa that illuminated chloroplast fragments can generate reduced TPN, which can then be used to drive a reductive carboxylation *via* the malic enzyme. The first section of the book closes with chapters by D. Herbert and M. Thomas on CO_2-organic acid studies in microorganisms and higher plants, respectively.

After two chapters on the more purely plant physiological aspects of photosynthesis by O. V. S. Heath, and by H. L. Penman and R. K. Schofield, there appear four valuable chapters on basic aspects of photochemistry as related to the problems of photosynthesis. The reviewer found these chapters (by M. G. Evans and N. Uri, by J. Weiss, by E. J. Bowen, and by J. Franck) to be the most rewarding of all in the book, since they present succinctly much important information not readily found elsewhere. Happily, the Emerson-Warburg controversy with regard to the quantum yield in photosynthesis is treated in a restrained manner in three chapters, one by Emerson and co-workers and two by Warburg and his colleagues. Neither protagonist in this dispute seems ready to admit defeat.

Chapters by R. Hill, by C. S. French and H. W. Milner, and by E. C. Wassink discuss thor-

[1] **Society for Experimental Biology.** 1951. [Symposia, vol. V.] Carbon dioxide fixation and photosynthesis. 342 pp. New York: Academic Press, $6.00.

oughly recent investigations on the nature of the photo-reduction accomplished by chloroplasts. B. Kok presents his interesting data supporting the idea that weak light affects respiration directly. If true, these observations might reconcile the divergent results of Emerson and Warburg on quantum yields in photosynthesis. They would also imply that photosynthesis is not merely the reverse of respiration, as it would appear to be from schemes presented by Calvin *et al.* The two chapters on the intermediary pathway of carbon in photosynthesis by Gaffron and coworkers, and by Calvin and his group show that a former disagreement between the two groups is resolved, and that phosphoglyceric acid is well established as a primary product in photosynthesis.

The book closes, as it began, with a chapter by H. A. Krebs, the final chapter discussing the use of Pardee's new CO_2-buffers in manometric experiments.

One's faith in symposia is bolstered by this book. There is, after all, something to be gained by joint discussion and presentation of data, and British scientists seem definitely to excel in the planning and production of significant symposia.

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Baxter, Dow Vawter. 1952. *Pathology in forest practice.* 2d ed., xiii + 601 pp., 224 figs. New York: Wiley. $7.50. The appearance of the second edition of this well-known book is welcome to all interested in forest pathology. The volume is again characterized by the large number of references made available that would ordinarily be overlooked. A minimum of space is given to mycology, pathological anatomy, fungus physiology, and other of the less applied phases of forest pathology, so that emphasis can be placed on the application of the knowledge of tree diseases to the practice of silviculture. In addition there is one chapter on diseases of shade and ornamental trees, while two chapters are devoted to decay, defects, and stains in forest products. Throughout the author has stressed the fact that often the basic cause of disease, even when a pathogen is involved, is a change in the ecological development of the species brought about by the activities of man. *J. S. Boyce.*

Milne, Lorus J., and M. J. Milne. 1952. *The biotic world and man.* xiv + 588 pp. New York: Prentice-Hall. $6.75. The latest addition to the endless series of general biology texts claims special notice here because of its ecological viewpoint. As Wheeler once remarked, natural history, is "the perennial rootstock or stolon of biological science," and the distinguished naturalist-authors of this textbook have succeeded surprisingly well in surveying the whole range of modern biology without losing their amateur standing. The volume is sumptiously illustrated, chiefly by the authors' photographs, which range from good to magnificent, and the text-figures, though regrettably diagrammatic in too many cases, are lively as well as new. The more esoteric aspects of physiology and biochemistry are not slighted, but nearly a third of the book is concerned with ecological matters, and it is clear that the authors are far more interested in the problems that confront intact animals and plants in a state of nature than in the rarefied problems of biology as seen by laboratory-bound investigators. This is as it should be, of course, and the text should provide genuine intellectual as well as esthetic pleasure to the students who use it.

Unfortunately, the teacher who "adopts" this text, if he cares for facts, will have to spend an inordinate amount of time correcting mistakes. Any book that covers so much ground is bound to contain errors and misleading statements, but this one has more than its share. Naturalists may perhaps be forgiven for believing that hemocyanin and hemoglobin contain the same hematin, but it is astonishing to find that the ecological sections are as full of misstatements as are the parts that are further from the authors' specialty. For example, the Colorado and the Mexican axolotl are confused, and the latter is said to have been kept by "Mayas and Incas"; the account of the evolutionary significance of the Galapagos is garbled, and the degree of faunal divergence within the islands is said to be correlated with distance from the mainland. The authors' grasp of geology is uncritical and inaccurate in general, and in their account of the Kaibab squirrel they seem to have accepted unquestioningly the recent newspaper stories about this animal and its habitat, for they repeat the fantastic statement that the species' isolation has lasted 40 million years. Glacial geologists will also be startled to learn that the Sahara was full of glacial meltwater during pluvial ages of the Pleistocene.

Howlers of this sort occur on nearly every page, but while this shows that the book was hastily written and not checked by critics, it does not follow that it is a bad book, designed to sell by virtue of its pictures. The basic plan is sound and challengingly new, and if its defects can be repaired in future editions the text will deserve the wide sale it is certain to have. *E. S. Deevey.*

Rothschild, Miriam, and Teresa Clay. 1952. *Fleas, flukes, and cuckoos. A study of bird parasites* [New Naturalist Special Volume]. xiv + 304 pp. London: Collins, 21 s.; New York: Philosophical Library, $8.75. As delightfully written and as well illustrated as its predecessors in this extraordinary series, this "New Naturalist" volume is especially noteworthy for the warm but unsentimental friendliness with which it approaches a widely unloved group of animals. The authors are both eminent parasitologists, and their respective specialties are happily blended here. Miss Rothschild's favorite animals, the bird fleas, are recent parasites in an evolutionary sense, being obviously derived from mammal fleas, and belong to a group that is relatively little modified for a parasitic existence. The bird-lice, Miss Clay's group, have proceeded much further down the road to completely dependent specialization. The two groups together expose most of the abstract problems and many of the practical ones that parasitology contains, and thus provide an admirable and novel introduction to the subject. As a treatise on parasitism the book spreads itself a little too widely, for the treatment of such large subjects as symbiosis and the brood-parasitism of cuckoos is inevitably thin. It is of quite unexpected value to the professional biologist, however, as the first comprehensive summary of the biology of arthropod parasites of birds. To insert into

a book of this character an almost monographic account of the receptaculum seminis of British bird fleas is a tour-de-force. The authors are to be congratulated equally for having written a popular book on parasites that completely avoids the sensational and the macabre.

For reasons best known to themselves the American publishers have quadrupled the price of the English edition. American ecologists will be well advised to order from an English bookseller. —*E. S. Deevey.*

Hyman, Libbie Henrietta. 1951. *The invertebrates: Platyhelminthes and Rhynchocoela, the acoelomate Bilateria* (Volume II); *Acanthocephala, Aschelminthes, and Entoprocta, the pseudocoelomate Bilateria* (Volume III). vii + 550, vii + 572 pp. New York: McGraw-Hill, $9.00 each volume. More than ten years after the publication of the first volume of Miss Hyman's incredibly ambitious undertaking, which was rightly hailed by a former editor of *Ecology* (*Quarterly Review of Biology,* **15**: 221–224) as "contemporary, authoritative, well-documented and in good prose . . . [occupying] a unique position on biological bookshelves," two more volumes have appeared in quick succession. The accelerated schedule can not be maintained, alas, for the two new volumes together represent Volume II of the original scheme, broken up for practical reasons. Further comments are probably superfluous; even notice of publication is probably unnecessary, for all zoologists who could afford it undoubtedly placed a standing order years ago. Those who did not need only to be told that the new parts live up to the brilliant standard set by Volume I (Protozoa through Ctenophora).

In these volumes all the "minor" or "lower" invertebrate phyla are treated with patience and scholarship that few people, professional zoologists included, realized before that they deserve. What is told about them is enormously interesting, but what cannot be told in the present state of zoological research is even more exciting; rewarding and "safe" Ph.D. thesis problems are hinted at on nearly every page. So well-studied a group of animals as the Trematoda is here shown to have been studied in a very one-sided fashion, the parasites of a few economically important vertebrates having received a disproportionate amount of attention. Nothing has been neglected, from the extraordinary disjunct geographic distribution of the freshwater entoproct Urnatella to the problem of learned behavior in flatworms, but Miss Hyman would be the first to admit that the treatise provides little beyond the bare summary that is essential for the guidance of future study. It is a measure of her achievement that the need for the remaining volumes is more desperate than it was before. If the Gastrotricha and the Priapulida offer such fascinating problems, what may a whole generation of zoologists not be missing in the study of arthropods and molluscs?

The publishers deserve a special word of commendation for their continued backing of this literally invaluable work, and for their efforts to keep the price within reasonable bounds. It is heartening to know that so prestigious a venture is economically sound. The whole biological world is grateful to Miss Hyman and only regrets that she is not multiple, so that the treatise could be completed in a shorter time. *E. S. Deevey.*